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A MULTIVARIATE  
EVOLUTIONARY ANALYSIS  
OF THE ANDEAN IGUANID LIZARDS  
OF THE GENUS STENOCERCUS

THOMAS H. FRITTS

SAN DIEGO  
SOCIETY OF NATURAL HISTORY

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Frontispiece. Open areas and exposed rocks on the steep valley walls of the Río Urubamba near Chilca, 1760m, Departamento Cuzco, Perú are inhabited by *Stenocercus ochoai*. At lower elevations of the Río Urubamba Valley, *S. ochoai* occurs in sympatry with *S. crassicaudatus*. Working on the bromeliad-covered slopes is William E. Duellman, of the University of Kansas who assisted with field work in southern Perú.

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## INTRODUCTION

Many approaches to the study of organic evolution have been explored since the dawning of Darwinian theory in 1859. A majority of the evolutionary studies prior to 1940 were based on empirical surveys of biological diversity and similarity. As a result of increased demands for scientific accuracy and greater understanding of some aspects of evolution, later studies emphasized experimental techniques and were more limited in scope than the more ambitious but less definitive earlier studies. However, the use of experimental methods often limits the number of parameters that can be studied and results in informative but disjunct analyses of evolutionary mechanisms. Results from diverse sources subsequently must be integrated and placed in a conceptual framework. Although the integration of information from diverse sources often places the evolutionary biologist on the margins of his personal competence, it is one of the most important functions he will perform in pursuit of increased understanding of organic evolution. In assuming the task of analysis and integration he must be "willing to err moderately often in order that inadequate evidence shall more often suggest the right answer" (Tukey, 1962).

Atchley (1971) used multivariate statistics to analyze simultaneously morphological and ecological data. Such techniques facilitate understanding of causal factors of morphological variation and are potentially useful in broader evolutionary studies (Atchley, 1970; 1971). Multivariate techniques can be applied in testing hypotheses as well as in heuristic studies. This multivariate study of the lizard genus *Stenocercus* is the result of my interest in the evolutionary interaction between ecological and morphological components in vertebrate populations. It is an attempt to integrate morphological, ecological, and behavioral data in a quantitative analysis of evolutionary trends in the Andean lizards of

the genus *Stenocercus*.

*Stenocercus* Duméril and Bibron (1859) is a member of the tropidurine group of the family Iguanidae, as defined by Etheridge (1964). The genus includes 29 nominate species distributed throughout the central Andes of South America at elevations of 200-3800 m. Some species of *Stenocercus* are comparable in their ecology to North American fence lizards of the genus *Sceloporus*, whereas others are more nearly equivalent to species in the North American genera *Sator* and *Petrosaurus*.

The purpose of this study is threefold: 1) to infer evolutionary events in the radiation of the genus *Stenocercus*) 2) to estimate ecological influence on past evolutionary trends and present distributional patterns; and 3) to integrate ecological and morphological data in defining adaptive abilities and in considering the evolutionary history in terms of niche theory (MacArthur and Levins, 1964). A heuristic approach is employed in the analysis in order to facilitate generation of testable hypotheses of evolutionary mechanisms. Conceptual aspects of niche theory and adaptive radiation are examined in the context of evolution within *Stenocercus*. A taxonomic revision of the genus is presented to facilitate discussion of the species.

A montane group was studied not only for physiographic and distributional diversity but also for faunal simplicity. At most Andean localities the fauna is small, and most elements are conspicuous and more easily studied than in more diverse lowland tropical regions. In addition, the close geographic proximity of ecologically divergent areas allows comparison of ecological factors with minimal geographic distortion. Lizards were studied because they have many morphological attributes that can be quantitatively measured, and because they can be observed and collected in reasonable series.

## ACKNOWLEDGEMENTS

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## MATERIALS AND METHODS

### MATERIALS

More than 1000 specimens of the genus *Stenocercus* were examined during this study. Of these, over 800 were collected and examined in life during 14 months of field work in the Andes of Bolivia, Ecuador, and Perú. Preserved material of every species recognized herein was examined; notes on coloration of living animals, colored photographs, and karyotypic materials are available for most species. Karyotypic studies will be the basis for a future report. A list of those specimens examined is given in Appendix A, whereas those specimens used in statistical analyses are indicated in Appendix B.

In most analyses emphasis is placed on the local sample in order to allow for consideration of climatic and ecological parameters measured at a specific locality. Except in certain cases a local sample is composed of four or more adult specimens of the same species collected within a five kilometer radius of a point. *Stenocercus roseiventris*, which is known largely from material collected before 1910 with general or imprecise locality data, is herein represented by two grouped samples from the Bolivian departments of Cochabamba and Santa Cruz. *Stenocercus moestus* is represented by a series of specimens with imprecise data. Other species for which local samples of four or more adult specimens are lacking are omitted from quantitative analyses.

Grouping of specimens from widely separated localities or different biogeographic or ecological environments was not done for several reasons. If the species does exhibit geographic variation in morphology, the statistical computations resultant from pooled samples will merely be reflective of the proportions of individuals from the various localities and habitats; the source of the variation—selection, drift, environmental influence—will not be detectable.

Although examples of pooling of samples are still common in zoological literature, the change in emphasis from consideration of geographic isolation and gene flow as primary evolutionary factors, to definition of selective pressures on local and microecological units will cause the decline of those practices that mask the causes of variation.

### DEFINITION OF CHARACTERS

The characters used in this study were chosen so as to measure as many attributes of the lizards as possible. Specific names for individual scales and characters based on specialized nomenclature have not been used for two reasons: 1) a generalized character, such as the number of scales between temporals (see definition below), can be compared among many groups having considerable variation in cephalic scutellation, whereas a character based on a particular type of scale, such as number of postoccipitals, depends upon the definition of homologous epidermal units and necessitates comparable nomenclature and cephalic patterns in all specimens studied; 2) the study of variation is facilitated by use of characters that involve counting or measuring morphological units quantitatively instead of grouping them into subjective classes.

Although meristic characters (scale counts) were preferred for quantitative study, some qualitative characters have been included. Since qualitative measurements involve grouping data into classes, considerable information can be lost if the grouping is not done carefully. Several of the characters treated qualitatively in the present study could be measured in a more quantitative manner with increased investment of time. The character based on the size of the lateral scales included two grouped classes: lateral scales which were greater than one-half the size of dorsals, and

lateral scales which were one-half the size of dorsals or smaller; the attribute could have been expressed as a measurement of the lateral scales or a ratio of laterals to dorsals. Characters measured qualitatively herein were of less value than they might have been if treated in a more quantitative manner. Twenty-nine characters were measured on each specimen used in statistical analyses, except in cases where specimens were damaged, thereby preventing observation of one or more attributes.

Aspects of coloration were compared for all populations for which notes on coloration in life were available. Of particular interest are sexually dimorphic characteristics. The ventral coloration of males is often markedly different from adult females, as well as from males of other species occurring in sympatry or in close geographic proximity. The ventral surfaces of the thighs and pelvic region are yellow or black in adult males of some species. The entire venter or that part lateral to a midventral stripe is brightly colored in some males. In the females of some species, the chin, side of head, and side of neck is black and in contrast to the ground color. Females of many species are similar in coloration, although differences do exist between them. The present analysis has not included any quantitative analysis of coloration due to the inherent problems of ontogenetic and sexual differences.

A brief description of the method used to measure each character employed in quantitative analyses is provided below, in order to facilitate understanding of the results and the design of comparative studies of related or similar groups of lizards.

*Scales Between Nasal and Subocular (NSO).*— The number of scales in contact with the supralabials between the subocular and the nasal is noted for both the right and left sides; the number used is the sum of the two sides. The elongate subocular and the nasal are not included. The subocular scale of *Stenocercus* is an elongate scale between the ventral margin of the eye and the supralabials.

*Supraoculars (SO).*— The number of supraocular scales in a transverse line at the greatest width of the supraocular semicircle is given. The supraoculars are approximately in longitudinal rows; therefore the character state is the maximum number of rows in one semicircle.

*Internasal Scales (IN).*— The number of scales between the nasals and in contact with the rostral varies from two to four.

*Scales Between Temporals (SBT).*— The number of dorsal head scales is counted along a transverse line between the temporal scales of the right and left sides and posterior to the interparietal. The counts originate and end with the row of angulate temporal scales posterior to the ultimate superciliary scale.

*Parietal Eye (PE).*— The presence or absence of a small unpigmented spot associated with the parietal eye is noted.

*Posterior Head Scales (PHS).*— The scales on the posterior part of the head are compared with the adjacent scales on the dorsal part of the neck.

*Scales Along Midline of Head (SMH).*— The scales along the midline of the head from the occipital region to the rostral are counted; the rostral is included.

*Head Scales (HS).*— The scales of the interorbital and frontal regions are noted to be smooth or keeled. Scales of the temporal region of nearly all species are keeled and are not recorded.

*Size of Scales Posterior to Dorsal One-half of Tympanum (SDT).*— The size of the scales posterior to the external auditory meatus is compared to the size of the adjacent scales of the dorsal neck. The scales posterior to the tympanum are considered to be small if they are one-half (or less) of the size of the dorsal neck scales.

*Type of Scales Posterior to Dorsal One-half of Tympanum (TDT).*— The scales in this region are recorded as granular, imbricate smooth, or imbricate keeled.

*Antehumeral Fold (AF).*— A fold of epidermis and dermis immediately anterior to the insertion of the forelimb is considered to be an antehumeral fold.

*Neck Fold (NF).*— The folds anterior to the antehumeral fold on the side of the neck are termed neck folds. In some species the neck fold and antehumeral fold are connected by a longitudinal fold.

*Auricular Lobules (AL).*— Some of the scales on the anterior margin of the tympanic opening are denticulate and project into the ear opening; they are termed auricular lobules. Repeated counts of the number of auricular lobules are variable and the character is considered to be of little utility.

*Posthumeral Pocket (PHP).*— A distinct depression or pocket of skin in the axillary region is termed a posthumeral pocket.

*Postfemoral Pocket (PFP).*— A distinct pocket or involution of skin behind the insertion of the hindlimb is termed a postfemoral pocket. Those species having a slight fold which is present only when the hindlimb projects posteriorly are considered to lack a postfemoral pocket.

*Condition of Dorsal Scales (DS).*— The dorsal scales are granular, imbricate smooth, or imbricate keeled. In species where two or more types of scales occur, the condition of the scales near the vertebral row is recorded.

*Condition of Lateral Scales (LS).*— The lateral scales are granular, imbricate smooth, or imbricate keeled.

*Size of Lateral Scales (SLS).*— The size of the scales on the sides of the body is compared with that of adjacent dorsal scales. Laterals one-half the size of the dorsals are noted as small.

*Vertebral Scale Row (VR).*— The row of scales on the middorsal line from the head to the base of the tail is termed the vertebral row. A partial or diverging row is recorded as a discontinuous vertebral row, whereas a row comprised of scales in a single unbroken line is considered as a continuous row.

*Dorsal Crest (DCT).*— A dorsal crest is recorded as present if the scales of the vertebral row are morphologically distinct from adjacent dorsals. The crest of some species is not raised above the adjacent

dorsals, whereas the crest of other species consists of high denticulate scales.

*Scales on Ventral Surface of Arm (VA).*— The scales of the ventral surface of the proximal forelimb are granular, imbricate smooth, or imbricate keeled.

*Scales on Posterior Thigh (PT).*— The scales on the posterior surface of the thigh are granular, imbricate smooth, or imbricate keeled.

*Subdigital Lamellae on Fourth Finger (LF).*— The subdigital lamellae are counted from the point of attachment of the third and fourth fingers to the terminus of the fourth finger.

*Subdigital Lamellae on Fourth Toe (LT).*— The subdigital lamellae are counted from the point of attachment of the third and fourth toes to the terminus of the fourth toe.

*Caudal Scales (CD).*— The size of the caudal scales and degree of keeling varies. Mucronate and conspicuously keeled caudals tend to be one and one-half times the size of ventral scales and are termed spinose. Smaller scales in relation to ventral scales have less prominent keels and are termed normal.

*Caudal Whorls per Autonomic Segment (AS).*— The position of autonomic planes of the caudal vertebrae is indicated by caudal whorls composed of larger scales than in other whorls. The number of caudal whorls or transverse rows of caudals between consecutive autonomic points is noted.

*Scales Around Middle of Body (SMB).*— The number of longitudinal rows of scales is determined by counting in a transverse line around the middle of the body halfway between the insertion of the limbs.

*Dorsal Scales in Transverse Rows (DTR).*— The dorsals are counted in a longitudinal paravertebral row from the occipital scales on the posterior margin of the head to the base of the tail at the posterior margin of the thigh.

*Scales Across Gular Region (SAG).*— The gular scales are counted in a transverse arch across the gular region from the ventral margin of one tympanum to the other. The scales of the chin are arranged in

longitudinal rows radiating from the labial region allowing precise counts of the number of rows transversed from one tympanum to another. The granular scales in the interior part of the tympanic depression are not included in the count.

#### DEFINITION OF ECOLOGICAL VARIABLES

An exhaustive analysis of the ecology of the lizards of the genus *Stenocercus* is not possible at present. All ecological data are examined on the level of the local sample in order to allow incorporation of variables pertaining to local demes instead of individual specimens. Meteorological data are taken from published records for Bolivia (Mendez, 1965), Ecuador (Garcia, 1959-1968), and Perú (Anonymous 1960-1963; 1964; 1965a; 1965b). Observations of local populations for periods of several hours to several days during field work are the basis for data on habitat preferences, associated fauna and flora, and behavior. Eight variables are employed in the quantitative analyses. A brief description of these variables is presented below in order to facilitate interpretation of the analyses. All meteorological variables are recorded as means of observations from two to ten years if data were available. Observations for one year are used for localities for which additional data are lacking.

*Maximum Precipitation in Any Month* (MXP).— The amount of precipitation for the one month of each year having the maximum rainfall was taken from meteorological records.

*Mean Monthly Precipitation* (MOP).— The mean monthly precipitation for a locality for each year was taken from meteorological records.

*Minimum Precipitation in Any Month* (MNP).— The amount of precipitation for the one month of each year having the minimum rainfall was taken from meteorological records.

*Mean Annual Temperature* (MAT).— In most cases the mean annual temperature was computed by averaging the mean monthly temperatures. For the few locali-

ties for which no temperature data are available, the mean annual temperature was computed using the relationship of 6°C per 1000 m (Eidt, 1969). Instead of using 30°C for the mean annual temperature at sea level for the basis of computations as proposed by Eidt, the actual mean annual temperature of a nearby locality in the same drainage system was used and corrected according to the difference in elevation between the two sites.

*Latitude* (LAT).— The latitude of each locality from which local samples were obtained was converted from degrees and minutes to degrees accurate to two decimal places.

*Altitude* (ALT).— The elevation at which the sample was collected is recorded in meters.

*Drainage* (DNG).— The location of each locality is noted as within the Atlantic or Pacific drainage system.

*Habitat* (HAB).— Lizards of a local sample are considered to be 1) terrestrial if individuals are observed on the ground as well as on exposed roots of shrubs and rock piles, 2) rock-dwelling if individuals of both sexes are confined to surfaces of rock piles and rock cliffs, or 3) arboreal if individuals of both sexes are frequently seen on vertical trunks or elevated branches of shrubs and trees.

#### UNIVARIATE METHODS

Basic statistics of all variables for each local sample were computed using a program written by Dennis M. Power. Intraspecific variation was examined by the Sum of Square-Simultaneous Test Procedure (SS-STP). The SS-STP is an *a posteriori* test of significance of means (Sokal and Rohlf, 1969) and defines nonsignificant subsets of samples after significant variance is demonstrated by an overall analysis of variance. The test is used for samples of only two means realizing that the probability of 0.05 is that of an *a priori* test, not an *a posteriori* test. Significance in analyses of only two samples is therefore tentative.

## QUANTITATIVE PHYLETIC METHODS

The quantitative phyletic algorithm (Kluge and Farris, 1969) was employed for evolutionary analysis of morphological relationships. The computer program adapted for use on the Honeywell-635 computer at the University of Kansas attempts to compute a most parsimonious rooted dendrogram from morphological data. The dendrogram is rooted by a set of characters considered to have been present in a common ancestor of the group. Selection of the characters to be used for the common ancestor is made on the basis of criteria outlined by Wagner (1961) and Kluge (1969). Although considerable discussion has centered around the subjectivity and circularity of these criteria for selecting characters present in ancestral forms, few alternatives exist (see Inger (1967), and Kluge and Farris (1969) for contrasting viewpoints of this problem.)

The criteria for selection of primitive (ancestral) character states (Wagner, 1961) likely to have been present in a common ancestor of all species in the genus *Stenocercus* are: 1) a primitive state is present in numerous representatives of closely related groups; 2) a primitive state is more widespread within the group than any one derived state; 3) a primitive state is one associated with states of other characters known to be primitive by other evidence. Although tentative ancestral character states can be assigned for most characters on the basis of criteria one and two, ancestral character states for those characters having a large range of states (e.g. scales around the middle of the body and scales across the gular region) must be inferred on the basis of criterion three. The concordance of criteria one and two in the selection of ancestral states for many characters of *Stenocercus* is possibly a result of the large size of the group being studied, as well as the similarity of the logic used in the formulation of the two criteria.

On the basis of both criteria one and two, the inferred ancestor possesses a low number of scales between the nasal and

subocular (6.5); a moderate number of supraoculars (5.0); a low number of internasals (2.0); a moderate number of scales across the occipital region between the temporals (10.0); a parietal eye in nearly all individuals (1.8); posterior head scales distinct from adjacent scales of dorsal neck; a moderately low number of scales between occiput and rostral (15.0); smooth head scales, small, imbricate, keeled scales on side of neck; antehumeral and neck folds; a few auricular lobules projecting into ear opening (2.0); no posthumeral pocket; imbricate, keeled scales on dorsum; imbricate keeled scales on lateral body which are nearly equal in size to dorsals; a continuous vertebral row; granular scales on posterior thigh; a low number of subdigital lamellae on fourth finger (18.0); a low number of subdigital lamellae on fourth toe (24.0); normal caudal scutellation; and three caudal whorls per autonomic segment.

On the basis of criterion one in concordance with criterion three the inferred ancestor has no postfemoral pocket; no dorsal crest; imbricate, keeled scales on ventral surface of proximal arm; a moderately low number of scales around the body (50.0); a moderately low number of dorsals between the head and the base of the tail (53.0); and a low number of scales across the gular region (24.0).

All of the above character states are tentative in being based on indirect evidence. Some of the character states are likely to be erroneous; however, if most of the inferred ancestral character states approximate those of an ancestral form, reevaluation of others with additional evidence will be possible.

The use of diverse kinds of morphological data in the quantitative phyletic program prompts consideration of weighting and scaling procedures. Kluge (1969) and Kluge and Farris (1969) discussed methods of weighting data for evolutionary analyses according to relative conservatism of a particular character in relation to others. The weighting function I use is one proposed by Kluge (pers. comm.) involving the formation of a ratio of interclass



variation/intraclass variation, or specifically, the standard deviation of the population means/the mean standard deviation of the individual populations. The weighting function, a real number, is multiplied by the value of the character state for each OTU (operational taxonomic unit). Each character has an independently computed weighting function. The purpose of the weighting function is to increase the relative number of estimated evolutionary steps between the states of a character in proportion to the conservatism of that character. The weighting function allows the conservative characters to have more influence in the evolutionary construct.

Kluge and Farris (1969) included diverse kinds of morphological characters in a quantitative phyletics analysis of the anurans, but all characters were coded and the ranges of character states were small and approximately equal. Most characters used by Kluge (1969) in a similar study of *Hemidactylus* were based on scutellational counts; only one character, "type of digit," included coded character states. The ranges of the populational means of the meristic characters varied; however, none of the characters included more than 15 evolutionary units before being weighted. Thus, the ranges of the characters within both of these data matrices analysed using the quantitative phyletic algorithm had comparable ranges.

The morphological data matrix used in this study includes several diverse kinds of characters. Both meristic characters, counts of the number of scales on a particular area of the body, and coded qualitative characters describing differences in scale pattern or morphology are utilized. The minimal number of states for a character is two (*e.g.* ventral scales smooth (1), ventral scales keeled (2)). The maximal number of states is 83 for the number of transverse rows of dorsal scales between head and base of tail (DTR). The number of character states observed in a character directly influences the respective weighting function computed for it. Thus, it is necessary to avoid duplication of this effect by rescaling all

observed character states to an approximate common range. This is accomplished by dividing all meristic characters by the minimal character state for that character. As a result most characters have a range of two. The characters are then weighted by multiplying the scaled values by the weighting functions. Other scaling techniques are possible but remain to be considered for use in similar analyses.

## MULTIVARIATE METHODS

Multivariate studies were performed using programs in the BMD (Biomedical Computer Programs) and SFA Program libraries at the University of Kansas Computation Center. Multivariate analyses using mean values for local samples were performed on 29 samples of 19 species, for which morphological, climatic, and ecological data are available. Matrices of product-moment correlation coefficients were computed for 28 morphological variables and eight ecological variables using the SFA 01C computer program. The two separate correlation matrices were factored independently through the use of the SFA 03D program of incomplete-components analysis. The vectors thus defined were subsequently rotated orthogonally according to the Varimax Criterion utilizing SFA 13B. Finally, factor scores were computed for both the ecological and morphological principal components analyses utilizing SFA 22C. The principal components analysis summarizes trends in the correlation matrix through the definition of vectors delineating maximal variance of the original matrix. Orthogonal rotation of the multivariate vectors insures independence of the trends defined. The computation of factor scores allows viewing of the individual OTUs on the vectors. Thus, each vector defined in the analysis can be described by its constituent OTUs in relative order and position. The eigen-value of each vector is a direct measurement of the amount of variance included in the vector; the eigen-vector is a description of the vector and indicates the relative amount each



character has influenced the delimitation of the vector.

Factor scores of the independently-factored morphological and ecological data sets for the 29 localities were analysed using a canonical correlation program, BMD X75. Canonical variables were computed for each canonical correlation.

Whereas principal components analysis attempts to explain maximal variance through transformation of original data into linear equations, canonical correlation attempts to find maximal covariance between two sets of data through delimitation of a series of linear equations. Canonical correlation analyses can compute as many correlations as there are variables in the smaller of the two data sets. All canonical correlations are statistically independent from others.

#### TAXONOMIC TREATMENT

The taxa assigned to the genera *Stenocercus* and *Ophryoessoides* were reviewed. Several species are included in *Stenocercus* that were previously assigned to *Ophryoessoides*. Generic assignment was made on the basis of morphological and ecological similarity within and between genera. The delimitation of species was

made on the basis of morphological concordance and ecological similarity between populations. The taxonomic treatment is necessarily a conservative one due to the paucity of material and rudimentary knowledge of the distribution and ecology of many species. Some populations are morphologically distinguishable from others of the same species but which are similar in most other aspects of distribution, ecology, and morphology. Sympatry between closely related species is rare, although better knowledge of the distributions of all species will likely provide examples of parapatric populations which do not interbreed and which warrant specific recognition. Geographic variation is discussed when samples are sufficiently large to allow statistical analysis.

The ranges used for meristic characters in the diagnoses are absolute ranges for all populations of the species. Individual populations are discussed when the population means are significant at  $p < 0.05$  level in SS-STP analyses. All means are computed for local samples and not for species. A mean character state for a species composed of more than one sample is of no statistical and little descriptive value. Taxa are listed in alphabetical order.

## RESULTS OF ANALYSES

Three major cladistic events are prominent in the evolutionary construct, resulting from the Wagner-tree analysis (Fig. 1). The right evolutionary branch includes nineteen populations of ten species. The species on the right branch in approximate order from basal to distal positions are: *Stenocercus ornatissimus*, *S. variabilis*, *S. humeralis*, *S. praeornatus*, *S. varius*, *S. boettgeri*, *S. simonsii*, *S. crassicaudatus*, *S. carriani* and *S. empetrus*.

The remaining OTUs are positioned on two major branches diverging near the ancestral condition. The central branch includes eight local samples of three species. In approximate order from basal to distal positions are OTUs of *Stenocercus melanopygus*, *S. moestus*, and *S. chrysopygus*. The left branch includes nine OTUs of six species. *Stenocercus orientalis*, *S. formosus*, *S. ochoai*, *S. roseiventris*, *S. marmoratus*,

and *S. cupreus* are represented by OTUs on the left evolutionary branch with the latter most distal from the ancestor. The left branch includes 273 patristic units, whereas the right branch has 473. The shorter and less diverse central branch includes 200 patristic units.

The 8 x 8 correlation matrix of ecological data for 29 local samples reflects several relationships among the variables. As elevation increases the minimum monthly precipitation in the year decreases. Mean annual temperature is inversely correlated with altitude; maximum and minimum monthly rainfall values are highly correlated with annual precipitation. Annual precipitation and maximum precipitation per month are correlated with mean annual temperature. Occupation of rock habitats by lizards is correlated with maximum monthly rainfall. In southern latitudes the lizards

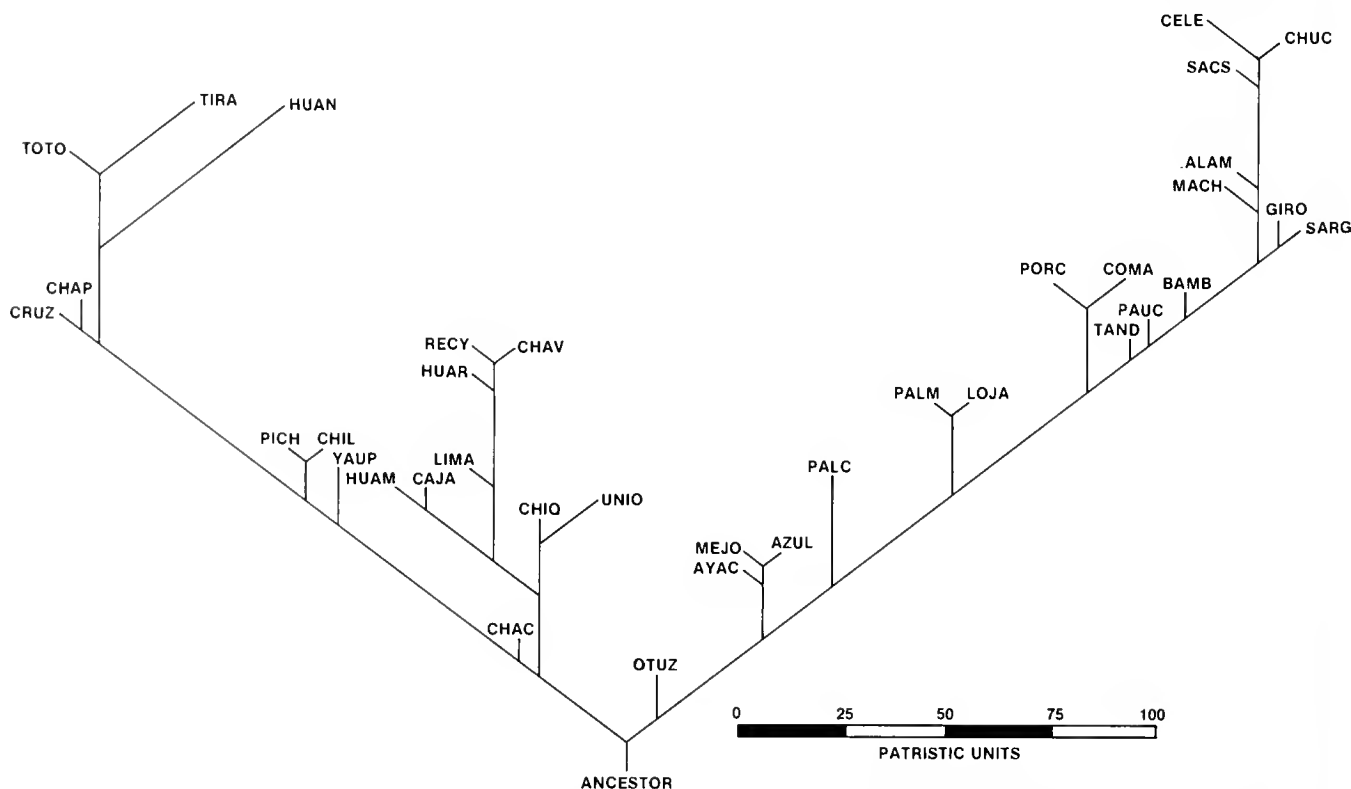


Figure 1. Wagner dendrogram of evolutionary relationships of 36 OTUs. See Appendix B for localities represented by OTUs.

occupy Amazonian slopes and interandean valleys, whereas in northern latitudes lizards occupy interandean valleys and Pacific slopes.

The principal components analysis of the ecological correlation matrix (Table 1) delineates three orthogonal factors "explaining" 81.4 percent of the original variance. The first factor "explains" 34.5 percent of the original variance and includes precipitation and habitat utilization. The second ecological factor "explains" 21.3 percent of the original variance and emphasizes relationships between latitude and drainage. The third ecological factor "explains" 25.5 percent of the variance and reflects the inverse relationship of altitude with mean annual temperature.

The 28 x 28 correlation matrix of the morphological variables indicates that meristic characters involving number of scales of a particular area or type are correlated; not all scale counts are positively correlated. The presence of a posthumeral pocket, postfemoral pocket, keeling on dorsal scales, and keeling on head scales correlate

Table 1.

Varimax Rotated Factor Matrix for 8 Ecological Variables. Factor loadings less than 0.25 are recorded as zero. Columns are factors; rows are variables. Columns two and three are transposed to facilitate visualization of the variables loading on the factors.

	1	3	2
MPX	0.923	0.	0.
MOP	0.843	0.339	0.279
MNP	0.758	0.469	0.
HAB	0.718	0.	-0.360
ALT	0.	-0.901	0.
TEM	0.	0.893	0.263
LAT	0.	0.	0.832
DNG	0.	0.	0.825
Cumulative Percent Variation "Explained"			
	34.55	60.08	81.40

with few other variables.

Six factors are defined from the 28 x 28 matrix of correlation coefficients of morphological variation through principal component analyses (Table 2). The six factors "explain" 82.9 percent of the original variance after orthogonal rotation. The first morphological factor "explains" 27.9 percent of the variance and emphasizes several characters measuring scale number and size, including aspects of the body and limbs. The variables measuring scale size are inversely correlated with those measuring the number of scales. The second morphological factor emphasizes characteristics of the tail and head and "explains" 17.8 percent of the original variance. The third factor is one reflecting trends in the dorsal crest and snout morphology; it "explains" 13.9 percent of the original variance. The percentage of the population with a parietal eye is inversely correlated with other characters emphasized in this factor.

The variation in thigh and head morphology is described by the fourth factor; 7.1 percent of the variance is accounted for by this factor. Characteristics of neck morphology are emphasized in the fifth factor; 11.2 percent of the total variance is "explained". The sixth factor accounts for only 5.1 percent of the total variance; aspects of the posthumeral pocket, posterior thigh, and dorsal scutellation are reflected in the factor. All other factors "explain" less than 5 percent of the original variance and are less interpretable.

Three relationships between the independently derived ecological and morphological factors are noted (Table 3). Scutellation (first morphological factor) is negatively correlated with latitude-drainage (second ecological factor),  $r_{ij} = .5476$ ,  $p < 0.01$  (Fig. 2). Thigh and head morphology (fourth morphological factor) are correlated with precipitation and habitat (first ecological factor),  $r_{ij} = .4263$ ,  $p < 0.05$ . Caudal and posterior head morphology (second morphological factor) are correlated with precipitation and habitat,  $r_{ij} = .3655$ ,  $p < 0.05$ .

Canonical correlations between morpho-

Table 2.

Varimax Rotated Factor Matrix for 28 Morphological Variables. Factor loadings less than 0.25 are recorded as zero. Columns are factors; rows are variables. Columns four and five are transposed to facilitate visualization of the variables loading on the factors.

	1	2	3	5	4	6
LF	0.904	0.	0.	0.	0.	0.
LT	0.853	0.	0.	0.	0.	0.
LS	-0.847	-0.359	0.	0.	0.	0.
VA	-0.839	-0.271	0.	0.	0.	0.
SAG	0.830	0.371	0.319	0.	0.	0.
SMB	0.794	0.	0.285	0.276	0.	0.
DTR	0.760	0.	0.330	0.313	0.	0.
SBT	0.653	0.561	0.	0.	0.	0.
AL	0.598	0.	0.	0.	-0.533	0.
PT	-0.568	0.	0.	0.	0.504	0.302
SO	0.532	0.308	0.	0.476	0.	0.
PHS	0.515	0.727	0.	0.	0.	0.
AS	0.	-0.919	0.	0.	0.	0.
CD	0.	0.905	0.	0.	0.	0.
SLS	0.403	0.684	0.345	0.	0.	0.
SMH	0.483	0.655	0.286	0.335	0.	0.
DCT	0.325	0.	0.765	0.	0.	0.351
IN	0.471	0.	0.754	0.	0.	0.
NSO	0.	0.409	0.740	0.	0.	0.
VR	0.324	0.	0.703	0.	0.	0.317
PE	0.	-0.362	-0.688	-0.445	0.	0.
PHP	0.	-0.299	0.588	0.	-0.461	-0.304
SDT	0.	0.	0.	-0.909	0.	0.
NF	0.	0.	0.	0.902	0.	0.
TDT	-0.436	-0.477	0.	-0.557	0.	0.
PFP	0.302	0.	0.	0.	0.765	0.
HS	0.	-0.420	0.	0.	0.645	0.
DS	0.	-0.252	0.	0.	0.	0.840
Cumulative Percent Variation "Explained"						
	27.86	45.63	59.60	70.73	77.84	82.89

Table 3.

Matrix of Correlation Coefficients of Three Ecological Factors with Six Morphological Factors. Critical value at  $p = 0.05$  level for correlation coefficients equals 0.367.

Ecological Factors	1	2	3
Morphological Factors			
1	0.25	-0.55	-0.29
2	0.37	-0.05	0.10
3	0.26	0.19	0.18
4	0.44	0.16	0.21
5	0.10	0.06	-0.12
6	0.05	-0.06	0.30

logical and ecological factors (Table 4) resemble the simple correlation described above. The signs after the factor names

indicate relationship of individual factors to the canonical correlation. Latitude-drainage (-) and altitude-temperature (-) show a positive relationship with thigh-head (-), scutellation (+), and crest-snout (-) morphology,  $R_c = .7434$ ,  $p < 0.05$ . Figure 3 illustrates the relative position of the OTUs in this canonical correlation. The second canonical correlation indicates that precipitation-habitat (+) and latitude-drainage (-) are correlated with scutellation (+) and tail-head (+) morphology,  $R_c = .6793$ ,  $p < 0.1$  (Fig. 4). The third canonical correlation is uninterpretable and does not approach significance.

Redundancy values for the first canonical correlation indicate that 33.4 percent of the ecological variance is "explained" by the morphological data; similarly 16.7 percent of the morphological variance is "explained" by the ecological data. Redundancy values for the second canonical correlation are similar, 33.2 and 16.7 percent, respectively.

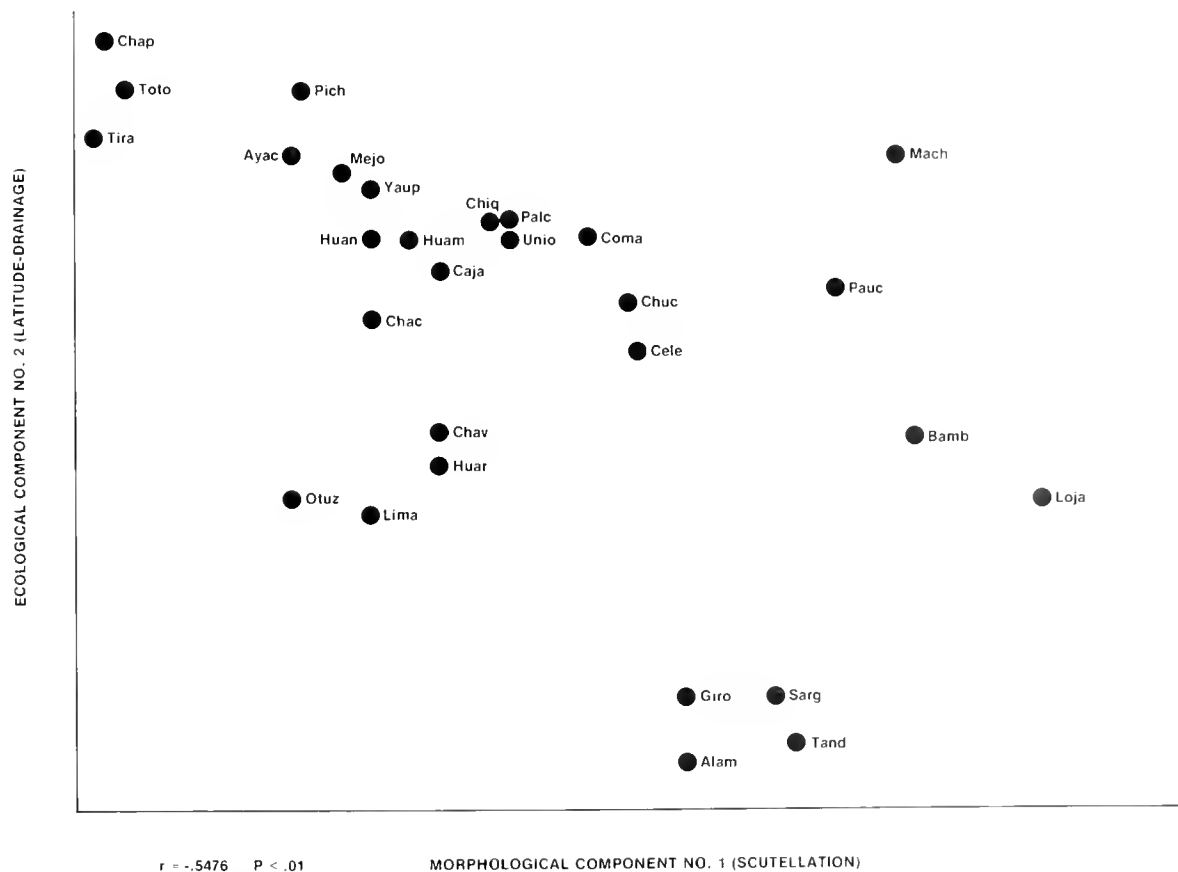


Figure 2. Correlation of first morphological component with second ecological component, based on 29 OTUs.

## DISCUSSION

The primary purposes of this study are the estimation of ecological and morphological variation, the definition of evolutionary trends, and the integration of evolutionary information and niche theory. Studies by Atchley (1970; 1971) and by Smith and Koehn (1971) are examples of recent attempts at integration of ecological and morphological data sets in a quantitative manner. Atchley (1971) studied intraspecific variation through multiple regression of morphological characters on climatic data. Smith and Koehn (1971) used species as the basic unit of studies and compared catostomid fishes through cladistic and multivariate analyses. The use of local samples as the basic unit in the present study is an attempt to incorporate intra- and interspecific

variation in the same analysis. Since selective pressures resultant from ecological and climatic factors can differ within the range of a species just as they differ from those of other species, simultaneous examination of intra- and interspecific variation can possibly contribute to our knowledge of factors causing speciation, as well as geographic variation below the species level.

## MORPHOLOGY AND CLADISTICS

The Wagner-tree (Fig. 1) computed for 36 local populations included in the present analysis depicts three major evolutionary lines. These lines represent computed cladistic lines and shall be treated separately in order to facilitate discussion of the various parameters of interest.

The right branch is composed of ten species of *Stenocercus*. All species assigned to the *S. humeralis* species group by Etheridge (1970) are positioned on the basal portion of the right branch. The most terminal OTUs of the right branch are members of the *S. crassicaudatus* species group of Etheridge. The most basal OTU on the right branch (OTUZ) represents *S. ornatissimus*, a member of the *S. chrysopygus* group. The populations of the right branch are mainly from high interandean and Pacific slopes of northern Perú and Ecuador with only the more basal ones from areas below 3000 m on Amazonian slopes of central Perú. *Stenocercus crassicaudatus* is the only species on the right branch that reaches southern Perú. *Stenocercus ornatissimus* occurs at intermediate elevations on the coastal slopes in northern Perú.

The central evolutionary branch includes three species, all members of the *S. chrysopygus* group as defined by Etheridge (1970). These species are distributed in coastal and interandean valleys of northern and central Perú. *Stenocercus melanopygus* (one of the species on the central branch)

Table 4.

Matrix of Canonical Correlations and Canonical Coefficients for Three Ecological Factors and Six Morphological Factors.

	Canonical Correlation		
	1	2	3
	0.743	0.679	0.303
Coefficients for Canonical Variables of Ecological Factors			
Factor 1	-0.515	0.811	-0.278
Factor 2	-0.592	-0.571	-0.569
Factor 3	-0.620	-0.129	0.774
Coefficients for Canonical Variables of Morphological Factors			
Factor 1	0.501	0.811	0.073
Factor 2	-0.299	0.458	0.012
Factor 3	-0.484	0.114	-0.142
Factor 4	-0.604	0.330	-0.152
Factor 5	-0.179	0.087	-0.509
Factor 6	-0.244	0.055	0.832

and *S. ivitus* (a closely related species not included in the analysis) are known to occur in sympatry with congeneric species of the right and left branches.

The left branch is composed of six species, all of which inhabit Amazonian drainages. The most basally positioned OTU (CHAC) represents *S. orientalis*, which occurs in northern Perú. The remaining OTUs on the left branch are from central and southern Perú and Bolivia. *Stenocercus orientalis* most closely agrees with the *S. chrysopygus* species group and is patristically close to the central branch. Intermediately positioned OTUs representing the species now known as *S. formosus* (Tschudi, 1845, *non* Boulenger, 1880) and *S. ochoai* have been placed in *Ophryoesoides* by previous workers. Populations of *S. roseiventris* and *S. marmoratus* are terminally

positioned on the left branch; both of the latter species were placed in the *S. crassicaudatus* species group by Etheridge. *Stenocercus cupreus*, also represented by a terminally positioned OTU, was placed in the *S. chrysopygus* species group.

The evolutionary construct agrees in several ways with the species groups proposed by Etheridge. Basic differences exist concerning the affinities of *S. roseiventris*, *S. marmoratus*, and *S. cupreus*. Whether the specialized caudal morphology shared by the latter three species is an example of parallel evolution with the species of the *crassicaudatus* group as indicated in the dendrogram or indicative of close relationships between them as indicated by Etheridge's classification will be discussed below.

In biogeographic terms the phyletic

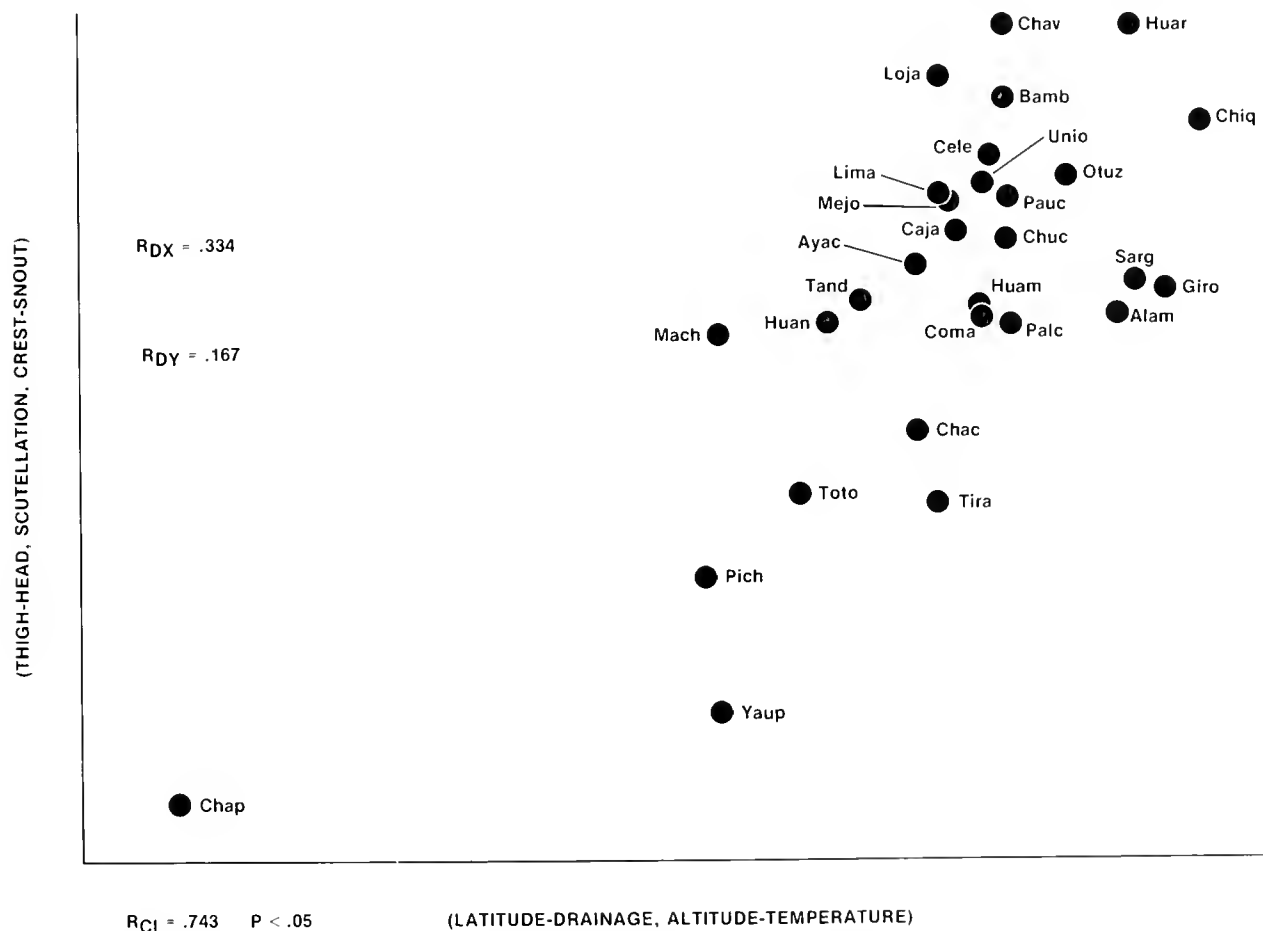


Figure 3. First canonical correlation between morphological data (abscissa) and ecological data (ordinate). Redundancy values ( $R_{dx}$  and  $R_{dy}$ ) are computed according to the method of Cooley and Lohnes (1972).

construct indicates different evolutionary lines in southern Amazonian regions and northern Pacific and interandean regions. Although several species located on the right branch have distributions extending from northern Perú to the region of the Nudo de Pasco in central Perú, none extends beyond the drainage of the Río Ene. *Stenocercus crassicaudatus* is the only species on the terminal right branch known to occur solely in central and southern Perú. The most basal OTUs of all branches tend to occupy xeric localities on coastal and interandean slopes. Terminal OTUs of all branches are confined to more mesic habitats at higher elevations in central and northern Perú and lower slopes of southern Amazonian regions. From a faunistic point of view, it can be noted that patristically close OTUs are allopatrically distributed, whereas

the known cases of sympatry involve species separated by large patristic distances.

Although consideration of distributional patterns, ecological trends, and previous evolutionary treatments are of value in evaluating an evolutionary construct, other more quantitative methods can be more informative. One way of looking at the data from a different point of view is to examine factor scores and vectors from a principal components analysis of morphological data. Principal components analysis allows definition of character trends through summarization of a correlation matrix of the data. These trends or factors are computed so that maximal variance is explained, and all factors of the analysis are not correlated with others. Evolutionary studies utilizing morphological data bases necessarily depend

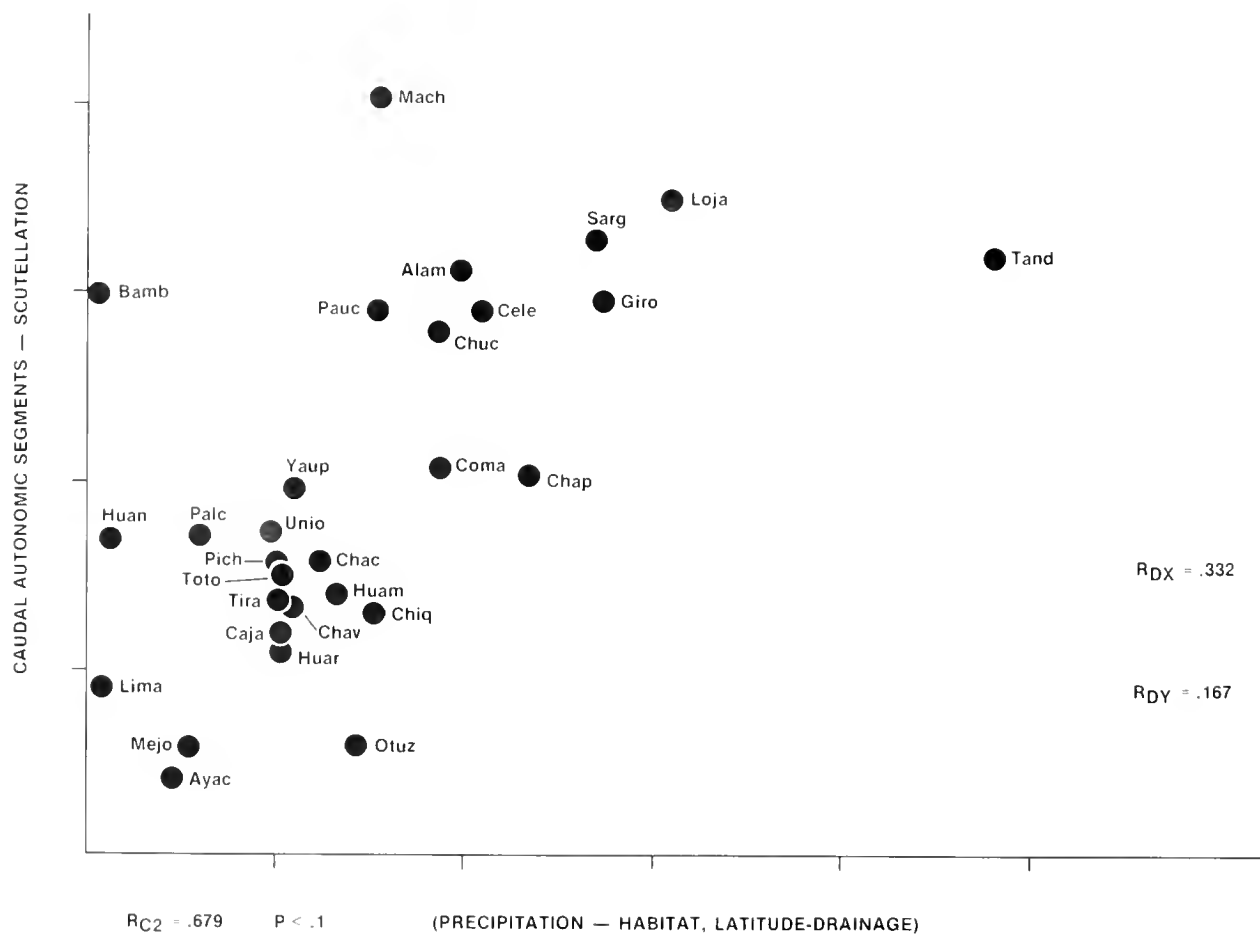


Figure 4. Second canonical correlation between morphological data (abscissa) and ecological data (ordinate). Redundancy values ( $R_{dx}$  and  $R_{dy}$ ) are computed according to the method of Cooley and Lohnes (1972).



upon correlations and concordant trends of groups of characters in order to estimate affinities. Because principal components analysis attempts to explain maximal variance by defining trends or factors, I hypothesized that the factors would define the major modes of adaptation. The radiation of a group into a different environment from the one for which it is adapted must necessarily involve considerable genotypic and phenotypic change. Similarly, the evolution of faunal complexity is known to necessitate genotypic and phenotypic modification, even when the local fauna is made up of competing taxa that are not closely related (MacArthur and Levins, 1964). It can be hypothesized that these adaptive genotypic shifts would account for major variational trends, whereas local variation, mosaic patterns, and minor adaptive changes would not.

In a study involving extensive faunal complexity with sympatry of ecologically similar but distantly related groups, the factors derived from principal components would be of more value in explaining ecological relationships than phylogenetic ones. An example might be a multivariate study of the trends in which seed-eating birds of an area differed. The trends which explain maximal variance would be those facilitating the avoidance of competition and successful occupation of the area while exploiting a common resource type.

However, in a study like the present one, in which the sympatric and parapatric species are evolutionarily closely related, the principal components would be of both evolutionary and ecological utility to the investigator. The hypothesis can be tested by comparing the grouping and ordering of factor scores for the OTUs on the individual vectors with patristic and cladistic events indicated on the evolutionary construct. Acceptance of the hypothesis should depend on two criteria: 1) the concordance of trends with cladistic and patristic events; 2) demonstrable association of distributional or ecological trends producing causal selective pressures. The latter is attempted through correlation of the morphological

factors with ecological ones.

It should be remembered that principal components are computed along axes of greatest variation of the data set, not any one character. Thus, OTUs positioned at opposite ends of the vector are most likely to differ in the particular set of characters emphasized by the vector.

On the scutellational vector (Fig. 5) the three OTUs having the highest factor scores are terminally located on the left evolutionary branch of the dendrogram; these OTUs have low scutellational values. The immediately adjacent OTUs on the vector include the remaining OTUs of the left branch in addition to two of the most basally positioned OTUs of the right evolutionary branch. The other end of the scutellational vector includes all terminally positioned members of the right evolutionary branch; these populations have high actual scutellational values. The OTUs positioned immediately on this vector are members of the central evolutionary branch and the most basal members of the right and left evolutionary branches. Thus, the scutellational vector is concordant with the large patristic distance between terminal right and left branches and approximates the cladistic event separating these two branches.

The second multivariate vector (Fig. 5) is one reflecting caudal morphology and cephalic scutellation. The three OTUs having the highest factor scores represent terminal members of the left branch except for *Stenocercus cupreus* (HUAN) which has a lower factor score. *Stenocercus cupreus* differs in several respects from the other species on the terminal left branch and has a large patristic distance from them. Adjacent on the second vector but distinctly separated are the most terminal right branch OTUs. Other OTUs are positioned on the lower end of the vector; these are patristically closer to the ancestral condition. This vector indicates a marked change from the ancestral condition in caudal and head morphology in terminal OTUs of the evolutionary construct; two groups are approximated on the positive

(upper) end of the factor. The positioning of the OTUs on this factor indicates a closer relationship between terminal members of the phyletic construct than the dendrogram illustrates or convergent (or parallel) evolution with regards to this subset of the data. The variance "explained" possibly reflects the change of head and tail morphology from the primitive condition to one or more derived sets of character states.

The third morphological factor describes dorsal crest and snout morphology (Fig. 6) and has OTUs less markedly grouped at extremes of the vector than previous factors. However, examination of the OTUs at the extremes of the vector is

informative. The populations having the highest factor scores are those basally positioned on the right and left branches of the dendrogram; those having the lowest factor scores include all members of the central evolutionary branch, except for CAJA which has a more intermediate factor score. The OTUs of the basal portions of the right and left branches are patristically similar to the OTUs of the central evolutionary branch but are those most diametrically positioned from OTUs of the central branch on this factor. Terminal OTUs of the right and left branches differ from the OTUs of the central branch on the basis of other factors, but are intermedi-

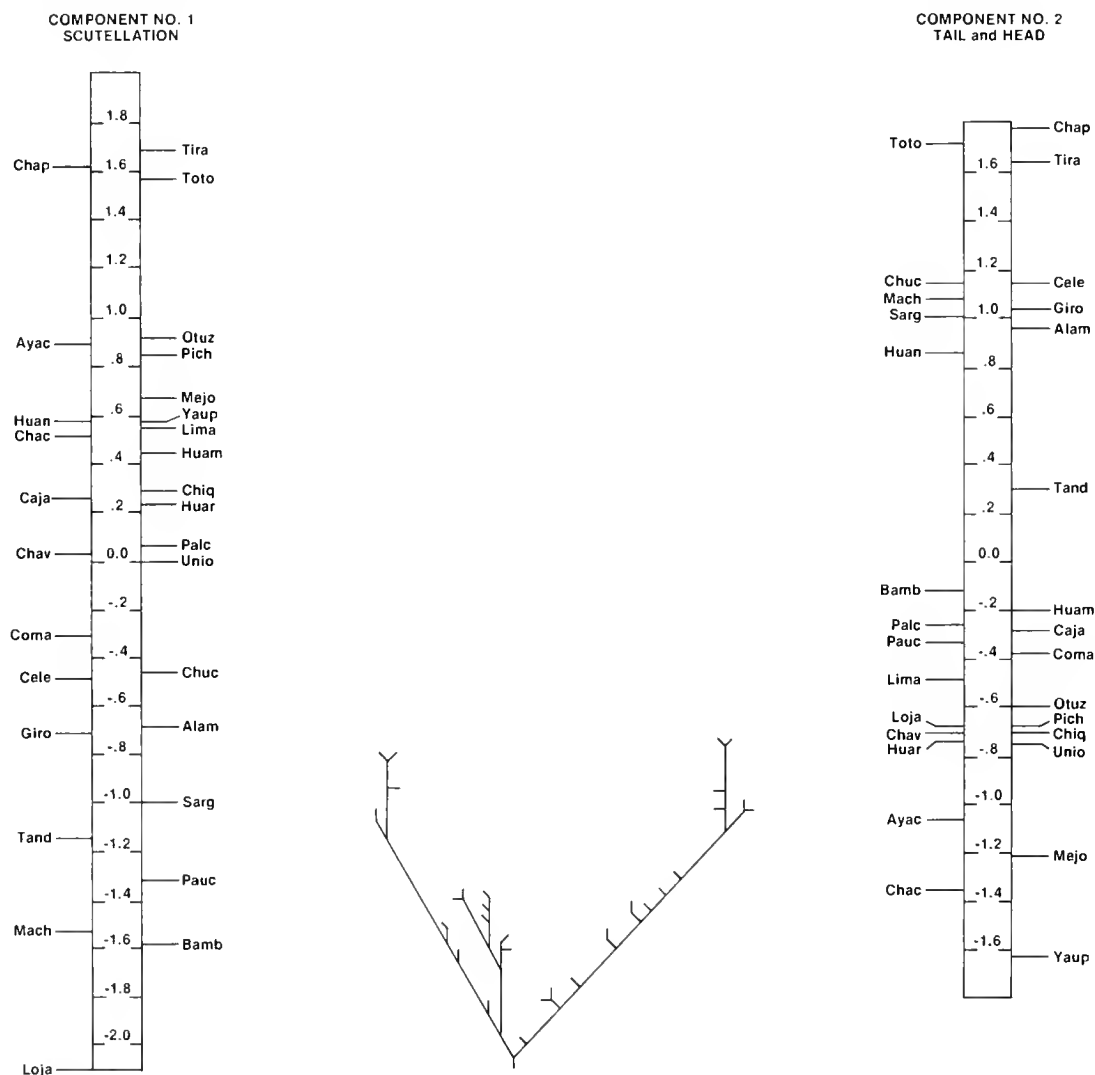


Figure 5. Diagrammatic representation of first and second orthogonal components of morphological data. Refer to Fig. 1 for position of OTUs on the dendrogram.

ately positioned on this factor. Thus, this factor is concordant with the cladistic event separating the right and left branches from the central branch.

The fourth morphological factor emphasizes thigh and head morphology (Fig. 6) and is of interest from two different viewpoints. The highest factor scores are those of basal and intermediate members of the left branch. The lowest factor scores are those of OTUs on the basal right branch. Terminal OTUs of the left branch also have lower factor scores than basal and intermediate OTUs of the left branch. On this factor, basal and intermediate OTUs of the left branch differ from the OTUs which are

patristically closest to them on the dendrogram. The most terminal OTUs of the left branch are from intermediate elevations of interandean and Amazonian slopes, whereas basal and intermediate members of the left branch are from lower elevations of Amazonian slopes. The OTU most closely positioned with basal left branch OTUs (those having high factor scores) is MACH which also occurs on moist Amazonian slopes. MACH, representing *S. crassicaudatus* and occupying an evolutionary position in the distal right branch, is the only OTU of that branch inhabiting southern Amazonian slopes. In this component it most closely resembles geographically and

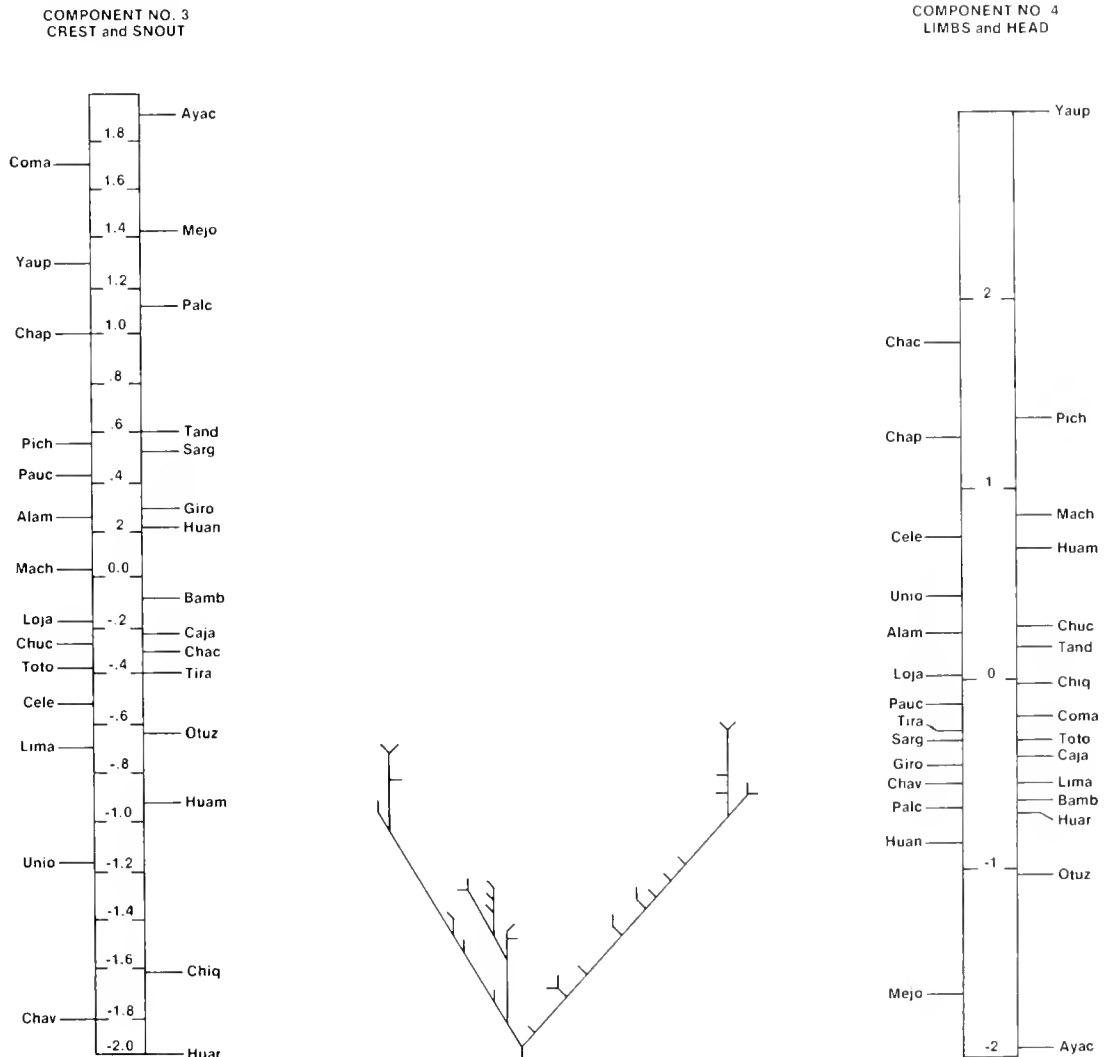


Figure 6. Diagrammatic representation of third and fourth orthogonal components of morphological data. Refer to Fig. 1 for position of OTUs on the dendrogram.

ecologically similar, but patristically distant, OTUs.

On the basis of neck morphology, which influences the fifth vector (Fig. 7), the most basal members of the central evolutionary branch are diametrically positioned from the most patristically similar OTUs on the terminal central branch. The former have the lowest factor scores for this vector; other central branch OTUs and basal OTUs of right and left branches have higher scores. This vector emphasizes morphological differences within the central evolutionary branch. Those OTUs with low factor

scores are the only members of the central branch known to occur in sympatry with other iguanid lizards. Although this factor serves to differentiate only a few taxa in the present sample, several species from Ecuador having neck morphology similar to the basal central branch OTUs remain to be added to the analysis. Several of the Ecuadorian taxa occur in sympatry with other iguanids, including other members of the genus *Stenocercus*.

The results of the principal components analysis tend to describe patterns similar to major cladistic and patristic events of the Wagner dendrogram. Each factor, in being independent of others, defines a different trend. Factors tend to differentiate between patristically close, but cladistically distinct, groups. This supports the hypothesis that the major factors will be ones describing evolutionary trends. The OTUs not involved in a particular divergence being defined, because of other aspects of their biology, would be expected to show little sensitivity to the variational trends accounting for major portions of the variance. The intermediate positions of distantly related species in some of the trends support this interpretation.

## MORPHOLOGY AND ECOLOGY

In order to examine further the relationships of the multivariate factors to evolutionary events and to estimate any adaptive shifts, ecological data are incorporated into the analysis. Factor scores for the multivariate factors derived independently from ecological and morphological data are examined for correlations. The significant correlation of trends in scutellation with latitude-drainage (Fig. 2) can be interpreted through examination of the individual variables. Lizards from southern Amazonian regions tend to have fewer scales than those from northern interandean and Pacific drainages. As noted above, the scutellational factor shows morphological differences between southern and northern species. Geographically intermediate regions are intermediate on the factor. Since this

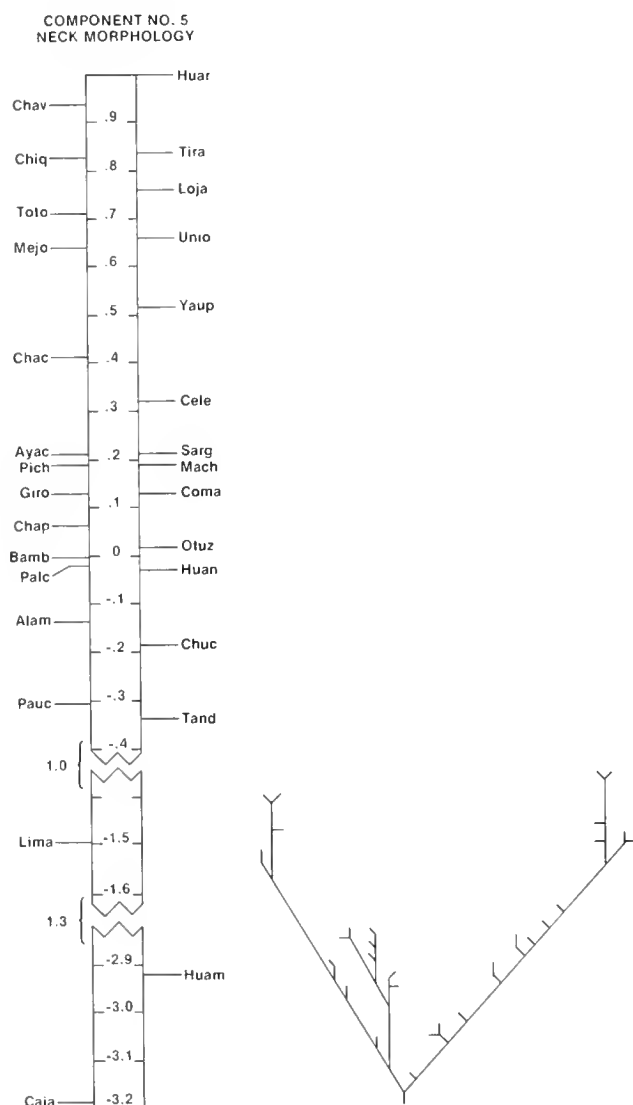


Figure 7. Diagrammatic representation of fifth orthogonal component of morphological data. Refer to Fig. 1 for position of OTUs on the dendrogram.

factor explains 28 percent of the morphological variance and is markedly concordant with the primary branching pattern of the dendrogram, further investigation of selective trends in scutellation is warranted.

Rock-dwelling species on the right branch occur largely in sympatry with congeneric species from the central or left branches. Rock-dwelling species on the left branch occur in sympatry with terrestrial or arboreal species of other iguanid genera. Comparison of sympatric pairs of congeneric species indicates in each case the two species are quite widely separated from each other patristically. Field observations indicate that each of the pairs includes one species that is basically terrestrial or confined to small solitary rocks in its activity. Both sexes of the other species feed and bask in large rock piles or on rock walls or rocky cliffs. In each case the terrestrial species occupies a basal position on the dendrogram, whereas the rock-dwelling species is more distally positioned.

## NICHE THEORY AND EVOLUTION

The canonical correlation analysis demonstrates a relationship between precipitation-habitat, latitude-drainage and morphological factors of tail, head, and scutellation. These same morphological factors are ones in which sympatric congeneric species differ abruptly. Those inhabiting rock habitats usually have more numerous head scales, larger mandibular musculature, spiny tails with a reduced number of caudal whorls per autonomic segment of the tail and more numerous scales on limbs and body. The occurrence of high factor loadings for precipitation and habitat variables in the first ecological factor does not mean that rock or elevated habitats are more common in moist areas, but that they are used more exclusively by species in moist areas. The occurrence of rock cliffs and outcrops depends largely on the geological characteristics of a locality, although precipitation and other climatic variables do influence weathering and soil formation. Although the more highly evolved species (distally posi-

tioned on dendrogram) are seldom seen feeding or basking in other than rock habitats, even when terrestrial species are rare or absent, the converse is observed. In localities where no specialized rock-dwelling species occur, the terrestrial, or less highly evolved species utilizes terrestrial as well as rock habitats for feeding and basking. Males show a preference for rock or elevated habitats, whereas females are predominant on the ground. For example, *Stenocercus ochoai*, in the Río Urubamba Valley of Perú, is found on the ground, on solitary rocks, and on large rock piles at localities where no other iguanid lizards occur. But where *S. ochoai* occurs in sympatry with the rock-dwelling species, *S. crassicaudatus*, *S. ochoai* is observed only on the ground and on low solitary rocks. Other species pairs have similar ecological relationships. In the terminology of Hutchinson (1957) the fundamental and realized niches of the rock-dwelling species are approximately equal (with reference to habitat), whereas the realized niche of terrestrial species in areas of sympatry with other iguanid species is a subset of the fundamental niche.

Although the terms generalized and specialized are often sources of confusion, I think that they describe the terrestrial and rock-dwelling species, respectively, with reference to both morphological attributes and ecological relationships. Utilization of terrestrial habitats can be observed in species at nearly every locality. Terrestrial species utilize terrestrial and rock habitats in allopatry or only terrestrial surfaces in allopatry or sympatry. Exclusive utilization of the rock habitat is confined to specialized species in more mesic areas.

Examination of these observations in the light of MacArthur and Pianka's (1966) comments on the optimal use of a patchy environment allows a testable hypothesis to be formulated with respect to distribution of sympatric species pairs and relative abundance of individual species. Among the factors they list for increased specialization are: 1) greater food density and 2) increased mobility of the animal in feeding activity. Studies by Terborgh (1971) in the Cordillera

Vilcabamba of Perú have shown increased species diversity and density of insectivorous birds on an altitudinal and moisture gradient. Other studies measuring general productivity along moisture gradients (Whittaker, 1970) have recorded increased productivity and energy flow with increased precipitation, especially at the lower extremes of such gradients. Since insects are important primary and secondary consumers, a similar increase in insect productivity and biomass might be expected in more mesic environments. Such an increase in insect abundance along a moisture gradient would result in greater density of food for insectivorous lizards.

Increased morphological specialization (e.g. increased number of toe lamellae) for mobility and efficiency of prey capture in a subset of habitat types would tend to increase the ability to obtain food. Although documentation is scant for lizards, studies by Collete (1961) and others have suggested selective pressures on such morphological attributes in nonterrestrial lizards. MacArthur and Pianka considered relative search and pursuit times for a species and reasoned that if search time is long, pursuit time must be relatively short; under such conditions the species loses little search time while pursuing prey. In an area of low food density, such a relationship would be advantageous. However, if pursuit time is long due to difficulty in reaching prey, or the percent of prey captured is low, a high food density resulting in low search time would be necessary for exploitation by a species as a coarse-grained resource. Such a relationship exists on the irregular and vertical surfaces of rock cliffs and rock piles.

The positive correlation between thigh-head morphology and precipitation-habitat indicates that lizards occurring in rock or arboreal situations and in more mesic localities possess smaller postfemoral pockets, fewer denticulate scales on the anterior margin of the ear and larger scales on the posterior thigh than terrestrial and more xeric adapted lizards.

Another morphological trend, caudal and cephalic morphology, is correlated with

precipitation gradients and habitat exploitation. All species with spinose caudal scutellation, except *Stenocercus cupreus*, frequent rock habitats and largely avoid activity on the ground surface. Species in which both sexes are known to frequent rock habitats in a coarse-grained manner (sensu MacArthur and Pianka, 1966) tend to lack parietal eyes, have more scales on the posterior margin of the dorsal head surface, smaller head scales, and smaller scales on the lateral body. Spinose tail scutellation is known in rock-dwelling lizards of several families (Bellairs, 1970). The reduction of lateral scale size may be adaptive in allowing the lizards to escape predators in rocks. Small scales allow the body to be inflated, wedging it within rock crevices and thus resisting extraction by predators. Similar behavior is known in *Cordylus* and *Uromastix* (Bellairs, 1970). The increase in number of head scales and decrease in size of the individual scales is accompanied by enlargement of the masseter musculature and head size in rock-dwelling species. In taking shelter in irregular crevices, biting may be a major defense of rock-dwelling lizards. Increased jaw musculature and head size would facilitate biting of a predator that could enter the confined spaces where these lizards hide. Little is known concerning the differences in physiology and basking behavior between rock-dwelling and more terrestrial lizards. Norris (1958; 1967) discussed thermoregulation and comparative aspects of behavior, habitat, and color pattern in relation to temperature. The loss of the unpigmented spot of the interparietal evidencing parietal position may be related to thermoregulatory differences between rock and ground dwelling lizards.

Since reduction of all original variables to a few robust multivariate variables would tend to limit flexibility of relationships defined between ecological and morphological data sets, canonical correlation is also employed. The first canonical correlation is defined between thigh-head, scutellation, crest-snout morphology, and latitude-drainage, altitude-temperature (Table 4), and emphasizes differences between left

branch OTUs and all others. Only the sample of *Stenocercus cupreus* (HUAN) approaches the cluster of right and central branch OTUs in position in Figure 3. OTUs from more southern Amazonian latitudes and in progressively lower and warmer environments exhibit aspects of scutellation, thigh-head and crest morphology that covary with environmental and biogeographic parameters. Recall that two of the morphological factors, scutellation and thigh-head morphology, emphasize differences between OTUs on the left branch and OTUs on other branches; the multiple correlation of these factors with distinctive environmental combinations and the grouping of OTUs on the left branch apart from central and right branches possibly indicate that these vectors are measuring variation resultant from adaptation to environmental and ecological parameters of southern Amazonian localities.

The second canonical correlation of scutellation and caudal-head morphology with precipitation-habitat and latitude-drainage (Table 4) is statistically independent of the previous canonical correlation. In this correlation (Fig. 4) OTUs in progressively more mesic and northern localities and those utilizing rock habitats display more marked specialization in scutellation and tail morphology than others. The terminal OTUs of the right evolutionary branch have the highest canonical scores for both the ecological and morphological data sets. OTUs on the basal right branch and those on the left and central branches have lower canonical scores for both data sets. Those OTUs on the left branch with specialized caudal and head morphologies are distinctly separated from, but are closest to, the terminal OTUs on the right branch. This relationship can be viewed in terms of sympatric relationships of the various OTUs with other iguanid lizards. Those OTUs in sympatry with other congeneric species occur in more mesic areas than those in allopatry. All of the pairs of sympatric species are composed of one species from the lowermost positions of Figure 4 (having generalized tail, head and

scutellational morphology and terrestrial in habitat preference in sympatry) and one other species from the upper right of Figure 4 (having specialized caudal, head and scutellational morphology, and occurring in rock or arboreal habitats).

Pursuit of prey on rock surfaces would involve more time and energy than on terrestrial substrates and consequently one would expect fewer successful captures per prey item sighted. Fine-grained utilization of terrestrial and rock habitats (in the frequency in which they are encountered) would be feasible in areas of low food density, such as xeric environments. Coarse-grained utilization of one or the other habitats through morphological and behavioral specialization would be adaptive only if food resources were sufficient or patch size large enough to reduce the necessity of migration from one patch to another (MacArthur and Levins, 1964; Levins, 1968).

Species of *Stenocercus* that are termed terrestrial species are generalized "searchers" exploiting open areas, bases of shrubs, and the smallest rock patches in sympatric situations, all areas where insects are low in density. In allopatry the terrestrial species treat habitat types as fine-grained resources, although males are more common on rock piles, and females are usually on the ground. The rock-dwelling lizards are found in moist areas where food density is sufficient to allow exploitation of rock habitats as coarse-grained resources. They are probably more efficient than terrestrial lizards in the pursuit of prey in such habitats.

Terminal members of the right and left branches are most patristically distant from the inferred ancestor and treat the patchy habit as a coarse-grained resource in utilizing only rock habitats. Most basal members of right and left branches as well as most members of the central branch occur in xeric habitats and utilize the patchy habitat as a fine-grained resource.

Whereas sexual dimorphism in size of adults of the rock-dwelling species is minimal, terrestrial species show marked

size differences between sexes. Sexual dimorphism in size has been shown by Schoener (1967) to be greater in areas where intraspecific competition is greater than interspecific competition. This possibly results in greater niche breadth. Lizards exploiting limited resources or having little interspecific competition for similar resources would tend to be sexually dimorphic in size, allowing each sex to prey on different sizes of food. The occurrence of sexual dimorphism in size in only those forms occurring in allopatric populations and those occupying terrestrial habitats indirectly supports the previous discussion of habitat exploitation in relation to productivity and food abundance. Food is abundant in rock habitats in mesic environments and rock-dwelling lizards are not sexually dimorphic. Food is scarce in terrestrial habitats causing intense intraspecific competition and favoring increased variation in size. Allopatric populations are largely confined to xeric environments which similarly have low food levels causing intraspecific competition and favoring increased variation in size, in this case sexual dimorphism.

The analysis of feeding habits of various species of *Stenocercus* will serve as a test of the hypothesis of fine-grained and coarse-grained use of habitat types. Quantitative measurement of food density in terrestrial and rock habitats at mesic and xeric localities should indicate greater food density in rock habitats and at mesic localities. Analysis of prey items of sympatric species will allow differences resulting from habitat selection to be substantiated. Similarly, differences in prey item size between males and females of sexually dimorphic species should exist. The food habits of *Stenocercus* are currently being studied in preserved material.

Another test of the hypothesis will be the addition of other species in the multivariate analysis. Similar ecological relationships should exist in other species

not previously analysed.

The convergent evolution of two groups of rock-dwelling lizards indicated in the evolutionary construct is understandable in terms of niche theory and resource utilization. The amount of precipitation on the Pacific slopes of northern Perú is positively correlated with altitude. The higher elevations are those with the most mesic conditions, and supporting sympatric species of *Stenocercus*. In the Amazonian slopes of southern Perú and Bolivia the amount of precipitation is more independent of altitude but tends to increase at lower elevations. The area around Cochabamba, Bolivia is an exception in having high rainfall at high elevations (Mendez, 1965). Terminal OTUs of the right branch of the dendrogram occur at higher elevations in northern Perú and southern Ecuador, and are sympatric with other species of *Stenocercus*. Terminal OTUs of the left branch are distributed at lower elevations on the Amazonian slopes of central and southern Perú and Bolivia. The OTUs representing *S. marmoratus* are from high altitudes of Bolivia in the extremely mesic region in the Departamento Cochabamba. Thus convergent evolution of the right and left branches toward a specialized morphology adaptive in different mesic environments is understandable. Both lines have evolved lizard species adapted for coarse-grained utilization of a patchy environment, the right branch species at high altitudes in northern Perú and southern Ecuador, and the left branch species at low elevations in southern Perú and Bolivia. Terminal members of the right and left branches are similar only in those aspects of morphology related to rock dwelling.

Both lines have resulted in some lizards exploiting rock habitats in sympatry with other iguanids. The evolution of faunal complexity, through evolution of sympatric species pairs includes much of the evolutionary change within the genus.



## EVOLUTIONARY CONCLUSIONS

Three evolutionary lines are delimited within *Stenocercus*. The right branch of the dendrogram contains species from central and northern Perú and from Ecuador. Basal members on the right branch are terrestrial species which occupy xeric environments and occur allopatrically in relation to other species of *Stenocercus*. Terminal members of the right branch are saxicolous (rock-dwelling) species inhabiting mesic environments at higher elevations and occurring in sympatry with other species of *Stenocercus* or other tropidurine genera. The central evolutionary branch includes species known to occur in sympatry with species on the terminal right branch. Some members of the central branch occur on the coastal slopes of central and northern Perú. Members of the central branch are terrestrial and patristically similar to the inferred ancestor.

The left evolutionary branch includes species inhabiting Amazonian slopes of Perú and Bolivia. Terminal members of the left branch are similar to those of the terminal right branch in occurring in mesic environments in sympatry with other iguanid lizards, in occupying rock habitats, and in having morphological adaptations for saxicolous habits. Species included in terminal positions on the right and left branches differ in most aspects of scutellation and are convergent only in those characteristics associated with saxicolous habits.

Basal members of the left branch are terrestrial and occur in allopatry or in sympatry with species on the terminal right branch. The evolution of rock-dwelling species occurring in sympatry with other species is likely in response to increased productivity in mesic environments. The presence of sexual dimorphism in size in terrestrial species suggests increased intra-specific competition for food in terrestrial habitats and indirectly supports the hypothesized relationship between productivity and grain size in habitat utilization. The

environment inhabited by *Stenocercus* is a patchy one in relation to rock outcrops and insect density. Evidence available suggests that allopatric species utilize the patchy habitat as a fine-grained resource in xeric areas where food density is low. Sympatric species are limited to mesic areas with greater food density and utilize patches in a coarse-grained manner.

The evolution of two groups of rock-dwelling lizards is likely a result of high productivity and food density in rock habitats in two different biogeographic zones, one in subtropical Amazonian lowlands and the other in temperate montane areas with high precipitation.

More detailed investigations are needed to measure the effects of variation in patch size and patch density. Some species, *S. guentheri* and *S. chrysopygus*, occur in allopatry at mesic localities where few rocks are exposed. Whether the size of rock patches is too small or rock patches are too infrequent to allow sympatric species to treat them as coarse-grained resources remains to be determined in a future study.

The evolution of the diverse genus *Stenocercus* has occurred in an ecologically mosaic region. The basic trend of evolution is from allopatrically distributed species in xeric environments to more specialized species occurring in sympatry in areas of high productivity and in allopatry in uniform or xeric environments. The restriction of *Stenocercus* to Andean regions indicates that most of the evolution of the genus likely occurred as a result of the Pliocene-Pleistocene orogenies of the central Andes. Ecological succession during early stages of mountain building likely progressed from xeric environments to geographically variable extremes of precipitation. The occurrence of alternating climatic shifts in tropical regions during the Pleistocene simultaneous with the last major uplift of the Andes results in a complex and still poorly understood history for the central

Andes (Vuilleumier, 1971). Present evidence indicates that climatic and ecological factors were of paramount importance in the evolution of *Stenocercus*. Future studies with emphasis on past and present ecology of the Andes should further understanding of the

evolution of montane tropical communities. Quantitative measurement of morphological and ecological variation and associated selective regimes with less emphasis on gene flow and geographic isolation is a short step toward such an understanding.

## TAXONOMIC ACCOUNT

Peters and Donoso Barros (1970) and Etheridge (1970) followed previous workers in considering the species of *Ophryoessoides* to be generically distinct from those of *Stenocercus* on the basis of the antehumeral, caudal and dorsal crest morphology. Some *Stenocercus* have large spinose caudal scales, whereas others have small imbricate caudal scales similar to those of all species presently included in the *Ophryoessoides*. Most species of *Stenocercus* have a conspicuous antehumeral fold, although one species is known to lack this fold. The majority of species of the genus *Ophryoessoides* have no antehumeral fold, but four do have a fold. Granular scales are present on the inner surfaces of antehumeral fold in all species of *Stenocercus*, except the single species lacking an antehumeral fold. Imbricate scales are found in the antehumeral region of most *Ophryoessoides*, although granular scales are known in three species. The dorsal crest is absent in some *Stenocercus*; the crest is present in all *Ophryoessoides*.

The above characters have been emphasized by previous authors (Etheridge, 1970, 1966; Boulenger, 1885) but no one character separates the two genera. Etheridge (1966) pointed out that several species previously considered to belong in *Ophryoessoides* or *Liocephalus* might be assignable to the genus *Stenocercus*. Within *Ophryoessoides* (sensu Etheridge, 1966) are several species occurring in lowland forested regions below elevations of 1000 m. These species have large supraoculars, large dorsal scales, keeled ventral scales

and relatively long and thin or laterally compressed tails. They also have inscrip-tional ribs which meet on the ventral midline; such an inscrip-tional rib pattern was noted by Etheridge (1965) as distinct from the pattern of other tropidurine genera and other species of *Ophryoessoides*. Most are arboreal. Included in this group is the type species of the genus *Ophryoessoides*, *O. tricristatus* Duméril (1851), as well as *O. aculeatus* (O'Shaughnessy, 1879), *O. caducus* (Cope, 1862), *O. erythrogaster* (Hallowell, 1856), *O. iridescens* (Günther, 1859b) and *O. scapularis* (Boulenger, 1901). The other species of *Ophryoessoides* resemble species of *Stenocercus* in having small supraoculars, smaller dorsal scales, smooth ventrals and in most species more robust tails. These species have inscrip-tional ribs which do not meet on the midventral line. These species of *Ophryoessoides* are largely confined to montane forests, grasslands and dry interandean valleys, as are most species of *Stenocercus*. They occupy the ground substrate or rock piles and seldom frequent tree trunks or tall shrubs.

Therefore, it is clear that some members of the genus *Ophryoessoides*, including the type species, differ in scutellation, rib morphology and ecology from other species included in the genus. These other species resemble species of *Stenocercus* in all of the above aspects of morphology and ecology. Thus, the present generic arrangement does not reflect the evolutionary affinity between montane *Ophryoessoides* and *Stenocercus*. The morphological divergence of lowland species of *Ophryoessoides*

from other tropidurines and especially from *Stenocercus* and montane *Ophryoessoides* casts doubt on their relationships within the tropidurine group of the Iguanidae. In order to present a taxonomic arrangement consistent with evolutionary relationships, as I understand them, redefinition of the genus *Ophryoessoides* is necessary. A more restricted genus including the lowland species and any other having the diagnostic characters presented herein is proposed.

### *Ophryoessoides* Dumeril, 1851

*Ophryoessodoides* Duméril, 1851:66 [Type species.—*Ophryoessoides tricristatus* Duméril, 1851, by monotypy].

*Brachysaurus* Hallowell, 1856:232 [Type species.—*Brachysaurus erythrogaster* Hallowell, 1856, by monotypy].

*Scartiscus* Cope, 1862:182 [Type species.—*Scartiscus caducus* Cope, 1862, by monotypy].

**Diagnosis.**— Small to moderate sized lizards having the following combination of character states: 1) interparietal small or absent; 2) supraoculars enlarged; 3) posterior head scales large; 4) antehumeral fold absent; 5) gular fold absent; 6) ventral scales keeled; 7) dorsal scales large, imbricate; 8) subdigital lamellae keeled; 9) femoral and preanal pores absent; 10) tail long, thin, or laterally compressed; 11) paired inscriptional ribs joining one another on midventral line; 12) sternal fontanelle large.

*Ophryoessoides* is the only tropidurine genus having pairs of inscriptional ribs joining at the midventral line (Etheridge, 1966). *Ophryoessoides* also differs from *Stenocercus* in having large posterior head scales, large supraoculars, and keeled ventrals.

**Content.**— As defined here, the genus contains six nominate species: *O. tricristatus* Duméril, *O. aculeatus* (O'Shaughnessy), *O. caducus* (Cope), *O. erythrogaster* (Hallowell), *O. iridescens* (Günther) and *O. scapularis* (Boulenger). Two undescribed species from Amazonian Perú possibly are members of the genus.

**Distribution.**— The species of the genus are known in peripheral Andean

regions from the Sierra Nevada de Santa Marta, Colombia (Ruthven, 1922), southward to Paraguay (Etheridge, 1970). Most species occur at elevations below 1000 m east of the Andes; however, *O. iridescens* inhabits the Pacific lowlands of Ecuador.

### *Stenocercus* Dumeril and Bibron, 1837

*Stenocercus* Duméril and Bibron, 1837:349 [Type species.—*Stenocercus rosei-ventris* D'Orbigny, 1837 in Duméril and Bibron, 1837, by monotypy].

*Trachycyclus* Duméril and Bibron, 1837:355 [Type species.—*Trachycyclus marmoratus* D'Orbigny, 1837 in Duméril and Bibron, 1837, by monotypy].

*Steironotus* (*Stenocercus*) Fitzinger, 1843:71 [Type species.—*Stenocercus rosei-ventris* D'Orbigny, 1837 in Duméril and Bibron, 1837, by monotypy].

*Heterotropis* (*Trachycyclus*) Fitzinger, 1843:71 [Type species.—*Trachycyclus marmoratus* D'Orbigny, 1837 in Duméril and Bibron, 1837, by monotypy].

*Scelotrema* Tschudi, 1845:154 [Type species.—*Scelotrema crassicaudatum* Tschudi, 1845, by subsequent designation Etheridge, 1970].

*Saccodeira* Girard, 1857:197 [Type species.—*Saccodeira ornatissima* Girard, 1857, by monotypy], new synonymy.

*Microphractus* Günther, 1859a:90 [Type species.—*Microphractus humeralis* Günther, 1859a, by monotypy].

**Diagnosis.**— Small to moderate sized lizards having the following combination of character states: 1) interparietal small or absent; 2) supraoculars not enlarged; 3) posterior head scales usually small; 4) antehumeral fold present or absent; 5) gular fold absent or if present caudal scales large and spinose; 6) ventral scales smooth or only weakly keeled; 7) dorsal scales small or moderate in size, those near middorsal region imbricate; 8) subdigital lamellae keeled; 9) femoral and preanal pores absent; 10) tail normal or spinose, not elongate or distinctly compressed laterally; 11) paired inscriptional ribs not joining one another on midventral line; 12) sternal fontanelle large; 14) free xiphisternal rods rarely present.

**Description.**— Lizards of the genus *Stenocercus* are small to moderate in size. The head scales are not well differentiated, and the interparietal is small or absent. A parietal eye is evidenced by an unpigmented spot on the interparietal of some species, but it is absent or only sometimes present in others. A continuous vertebral scale row is

present or absent and in some species is modified so as to form a distinct dorsal crest. The dorsal scales are imbricate over the entire dorsum or only in the paravertebral region. The lateral body scales are nearly equal in size to the dorsal scales or are much smaller. An antehumeral fold lined with granular or imbricate scales is present only in some species. The scales on the posterior surfaces of the thighs are imbricate or granular. The caudal scales are imbricate, keeled, enlarged, and spinose. The species with spinose tails usually have only two whorls of scales between autonomic points of the tail. Femoral and preanal pores are absent. Males of many species have yellow or black coloration on the ventral surfaces of the thighs and pelvic

region. Sexual dimorphism in dorsal and ventral coloration is present in some species.

*Content.*—Twenty-nine nominate species are assignable to the genus as presently defined. Two additional species are known but remain unnamed due to the lack of adequate material and distributional data. Whereas some species of *Stenocercus* have been included in the genus since their original descriptions, others have been considered to be in separate genera. In addition to the genera considered synonymous with *Stenocercus*, species have been cited most often in combination with the generic names *Liocephalus*, *Ophryoessoides*, and *Proctotretus*.

#### Key to Species of *Stenocercus*

- 1) Scales on posterior surface of thigh imbricate .....2  
Scales on posterior surface of thigh granular .....12
- 2) Caudal scales large, nearly twice the size of ventrals, two caudal whorls per autonomic segment .....3  
Caudal scales small, approximately equal in size to ventrals, three or four caudal whorls per autonomic segment .....4
- 3) Vertebral row discontinuous, inconspicuous; scales around midbody fewer than 55 .....*S. marmoratus*  
Vertebral row continuous, forming prominent dorsal crest; scales around midbody more than 53 .....  
*S. roseiventris*
- 4) Antehumeral fold present .....5  
Antehumeral fold lacking .....8
- 5) Neck folds present anterior to antehumeral fold .....6  
Neck folds lacking .....7
- 6) Three caudal whorls per autonomic segment; scales around midbody fewer than 71 .....*S. ochoai*  
Four caudal whorls per autonomic segment; scales around midbody more than 75 .....*S. formosus*
- 7) Antehumeral fold conspicuous, lateral venter of males not red or pink, no posthumeral pocket .....  
*S. nigromaculatus*  
Antehumeral fold weak, lateral venter of males bronze-red, deep posthumeral pocket .....*S. ornatus*
- 8) Occipital scales larger than other head scales, wider than long, posterior margin bluntly curved .....*S. apurimacus*  
Occipital scales subequal to other head scales, not bluntly curved on posterior margin .....9
- 9) Scales around midbody 60 or more .....*S. guentheri*  
Scales around midbody 60 or fewer ...10
- 10) Gular region of males black, chin usually not black; venter of males not pink; posthumeral pocket weak or moderately developed .....11  
Gular region of males pink; venter of males pink with black midventral stripe from pectoral region to ventral thighs; posthumeral pocket deep .....*S. rhodomelas*
- 11) Ventrals weakly keeled; pectoral region of males pink; posthumeral pocket lacking .....*S. trachycephalus*  
Ventrals smooth in adults, weakly

- keeled in juveniles, pectoral region light pink, yellow or black; posthumeral pocket present ..... *S. festae*
- 12) Caudal scales large, nearly twice the size of ventrals, two caudal whorls per autonomic segment ..... 13  
Caudal scales small approximately equal in size to ventrals, three caudal whorls per autonomic segment ..... 17
- 13) Vertebral row discontinuous ..... 14  
Vertebral row continuous from neck to base of tail ..... 15
- 14) Caudal whorls subequal in size .....  
*S. empetrus*  
Caudal whorls alternating in size, smaller whorls one-half size of adjacent whorls ..... *S. carrioni*
- 15) Scales of vertebral row similar to adjacent dorsals not forming distinct dorsal crest, scales around midbody fewer than 65 ..... *S. cupreus*  
Scales of vertebral row distinct from adjacent dorsals, forming low dorsal crest; scales around midbody more than 70 ..... 16
- 16) All dorsal scales imbricate; dorsals meeting smaller lateral scales abruptly in dorsolateral region ... *S. simonsii*  
Dorsals near vertebral row imbricate, dorsals near dorsolateral region smaller, granular; dorsals gradually reduced laterally, grading into granular lateral scales ... *S. crassicaudatus*
- 17) A neck fold anterior to antehumeral fold present ..... 20  
Neck fold lacking ..... 18
- 18) Scales around midbody fewer than 40 ..... *S. moestus* (part)  
Scales around midbody more than 40 ..... 19
- 19) Antehumeral fold lacking ..... *S. ivitus*  
Antehumeral fold present .....  
*S. melanopygus*
- 20) Scales of vertebral row morphologically distinct from adjacent dorsals, forming a dorsal crest ..... 25
- Scales of vertebral row not morphologically distinct from adjacent dorsals, no dorsal crest ..... 21
- 21) Scales posterior to tympanum granular, head scales smooth .....  
*S. chrysopygus*  
Scales posterior to tympanum imbricate; head scales keeled or smooth ..... 22
- 22) Head scales keeled ..... *S. orientalis*  
Head scales smooth ..... 23
- 23) Scales across gular region between tympana fewer than 30 ..... 24  
Scales across gular region between tympana more than 35 ..... *S. haenschi*
- 24) Scales around midbody fewer than 40 .....  
*S. moestus* (part)  
Scales around midbody more than 45 .....  
*S. ornatissimus*
- 25) Scales around midbody fewer than 75 .....  
*S. variabilis*  
Scales around midbody more than 75 ..... 26
- 26) Black bar on ventral neck of males .....  
*S. praeornatus*  
No black bar on ventral neck of males ..... 27
- 27) Black midventral stripe in males .....  
*S. nubicola*  
No midventral stripe in males ..... 28
- 28) Subdital lamellae of fourth toe more than 35; scales around midbody more than 99 ..... *S. humeralis*  
Subdigital lamellae of fourth toe 35 or fewer; scales around midbody fewer than 99 ..... 29
- 29) Posterior head scales morphologically distinct from adjacent scales of neck; one row of supraoculars between largest supraocular row and posteromedial border of semicircle .....  
*S. boettgeri*  
Posterior head scales similar to adjacent scales of neck; two rows of supraoculars between largest supraocular row and posteromedial margin of semicircle ..... *S. varius*

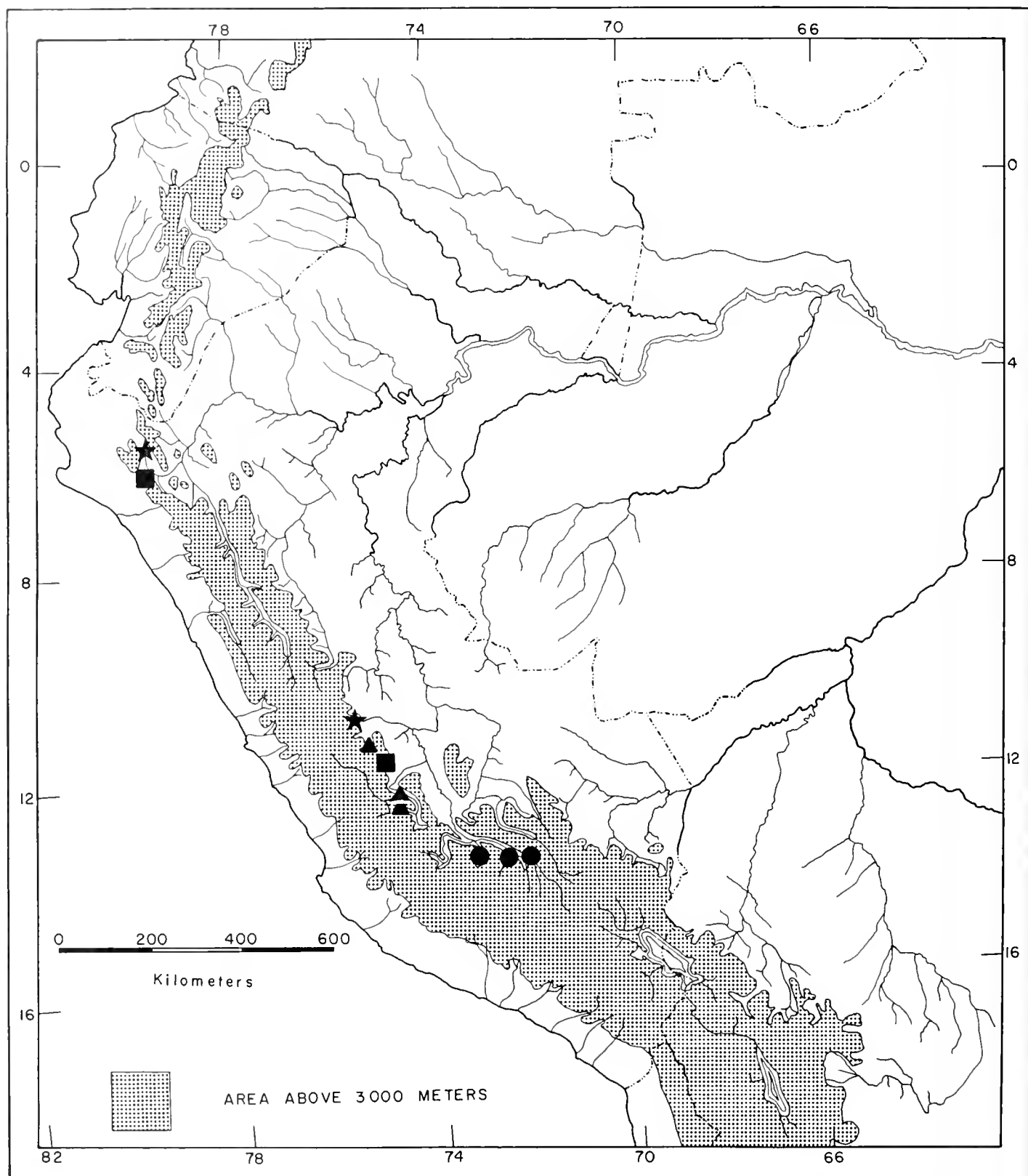


Figure 8. Distribution of *Stenocercus apurimacus* (circles), *S. praeornatus* (squares), *S. variabilis* (triangles) and *S. boettgeri* (stars) in the Peruvian Andes.

*Stenocercus apurimacus*

Fig. 38

*Stenocercus apurimacus* Fritts, 1972:2.

Type Material.— Holotype KU 134273 and paratypes KU 134270-134272, 134274-134309 from Puente Pachachaca, 15 km W Abancay, 1800m, Departamento Apurimac, Perú.

**Diagnosis.**— 1) Posthumeral pocket deep; 2) postfemoral pocket absent; 4) scales posterior to tympanum keeled, imbricate, equal in size to dorsal neck scales; 5) scales on posterior thigh keeled, imbricate; 6) vertebral row continuous, forming high dorsal crest extending onto tail; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 48-61; 11) scales across gular region between tympana 18-26; 13) venter of males gray-beige to gray with a blue hue; 17) posterior head scales large, wider than long, rounded posteriorly, a pair of large parietals in broad contact posterior to small interparietal. *Stenocercus apurimacus* is the only species of *Stenocercus* occurring in southern Perú which lacks antehumeral and neck folds.

**Distribution.**— The species is known in Perú from elevations of 1800-2700 m in the interandean valleys of the Río Apurimac and Río Pachachaca in the departments of Cuzco and Apurimac (Fig. 8).

**Ecological Observations.**— The species occurs on the ground and on rocks in xeric habitats where *Acacia*, thorn shrubs and cactus form the predominant plant cover. *Stenocercus apurimacus* occurs in sympatry with *S. ochoai* at Curahuasi, 2700 m, Departamento Apurimac.

**Remarks.**— Variation in the number of scales around the body and chin coloration was described by Fritts (1972).

*Stenocercus boettgeri* Boulenger

Fig. 35

*Stenocercus boettgeri* Boulenger, 1911:22.

Type Material.— Syntypes BMNH 1911.12.13.25-32 (RR 1946.8.11.92-99) from Huancabamba (Departamento Piura), Perú.

**Diagnosis.**— 1) Posthumeral pocket

absent; 2) postfemoral pocket present; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming indistinct dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 78-91; 11) scales across gular region between tympana 43-55; 16) one row of supraoculars between largest row of supraoculars and posteromedial margin of semicircle; 17) scales across occipital region similar to other head scales, distinct from dorsal neck scales; 18) scales of nasal region large.

*Stenocercus boettgeri* and *S. varius* have common ranges for several scutellational characters. They can be distinguished by the following characters: the scales between the nostrils of *S. boettgeri* are large; those of *S. varius* are smaller and more irregularly positioned. The largest supraocular row is separated from the interorbital scales along the posteromedial margin of the semicircle by one small supraocular row in *S. boettgeri*; two small supraocular rows lie between the largest supraocular row and the posteromedial interorbital scales in *S. varius*. The scales of the posterior margin of the dorsal surface of the head are notably larger in *S. boettgeri* than in *S. varius* (Fig. 10). The posterior head scales of *S. varius* are small and nearly granular, thereby resembling the dorsal neck scales.

**Distribution.**— *Stenocercus boettgeri* is known from the Amazonian drainage of central Perú (Paucartambo, 2900-3250 m, Departamento Pasco) and from extreme northern Perú (Huancabamba, Departamento Piura, at approximately 3000 m). Several species of *Stenocercus* are known to occur in the area between the extremes of the range of *Stenocercus boettgeri*, but no specimens of this species are known from the intermediate localities (Fig. 8). Due to inaccessibility, the eastern margins of the Río Marañón remain poorly known and may eventually prove to support geographically

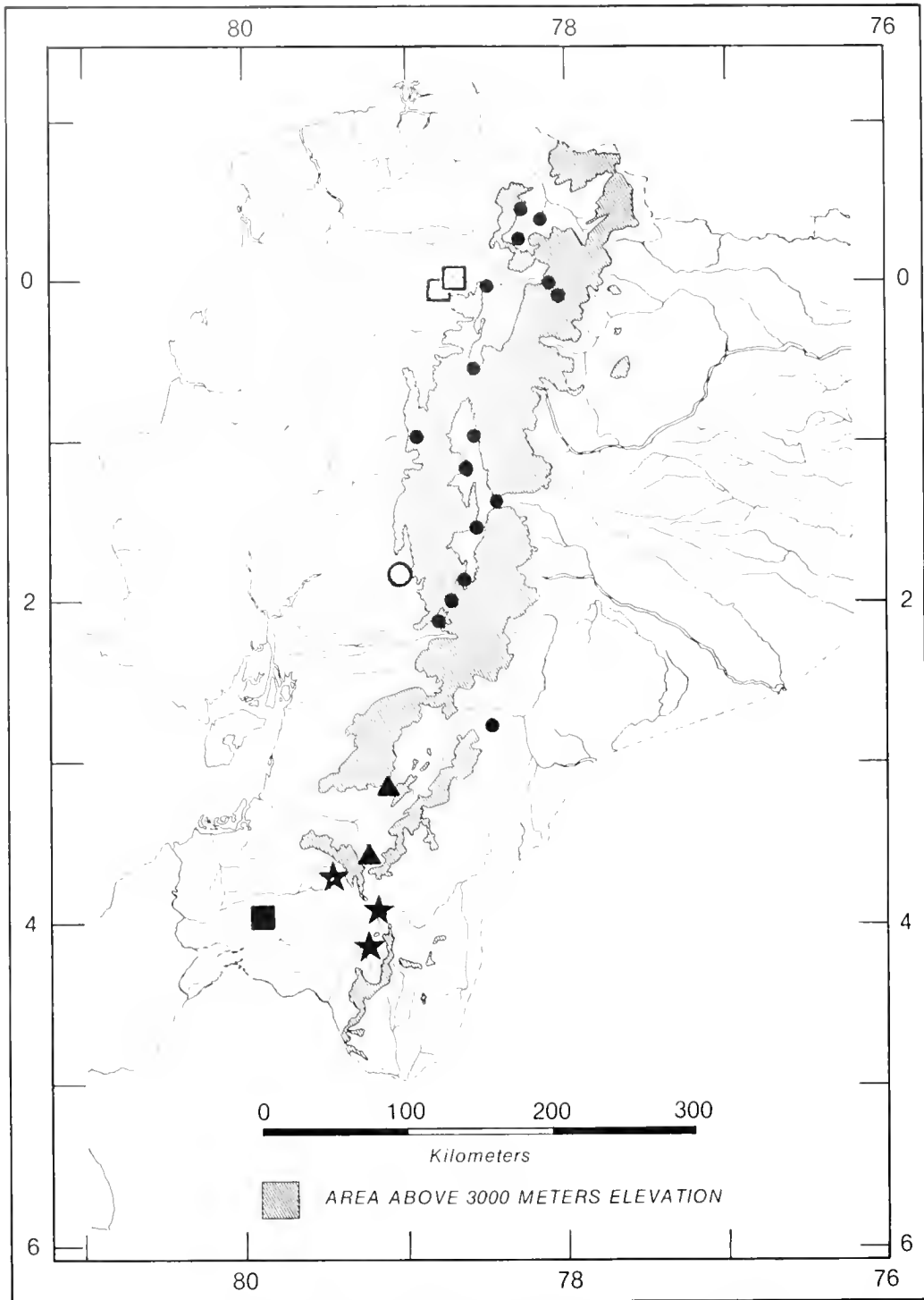


Figure 9. Distribution of *Stenocercus guentheri* (closed circles), *S. haenschi* (open circles), *S. carrioni* (closed squares), *S. varius* (open squares), *S. simonsii* (triangles) and *S. humeralis* (stars) in the Andes of Ecuador.

intermediate populations of the species. The large distance between the populations from Piura and Pasco departments extends from the northern tributaries of the Río Marañón

valley across the Río Huallaga drainage and into the upper regions of the Río Perene.

*Ecological Observations.*— Individuals of both sexes are active on large rock piles



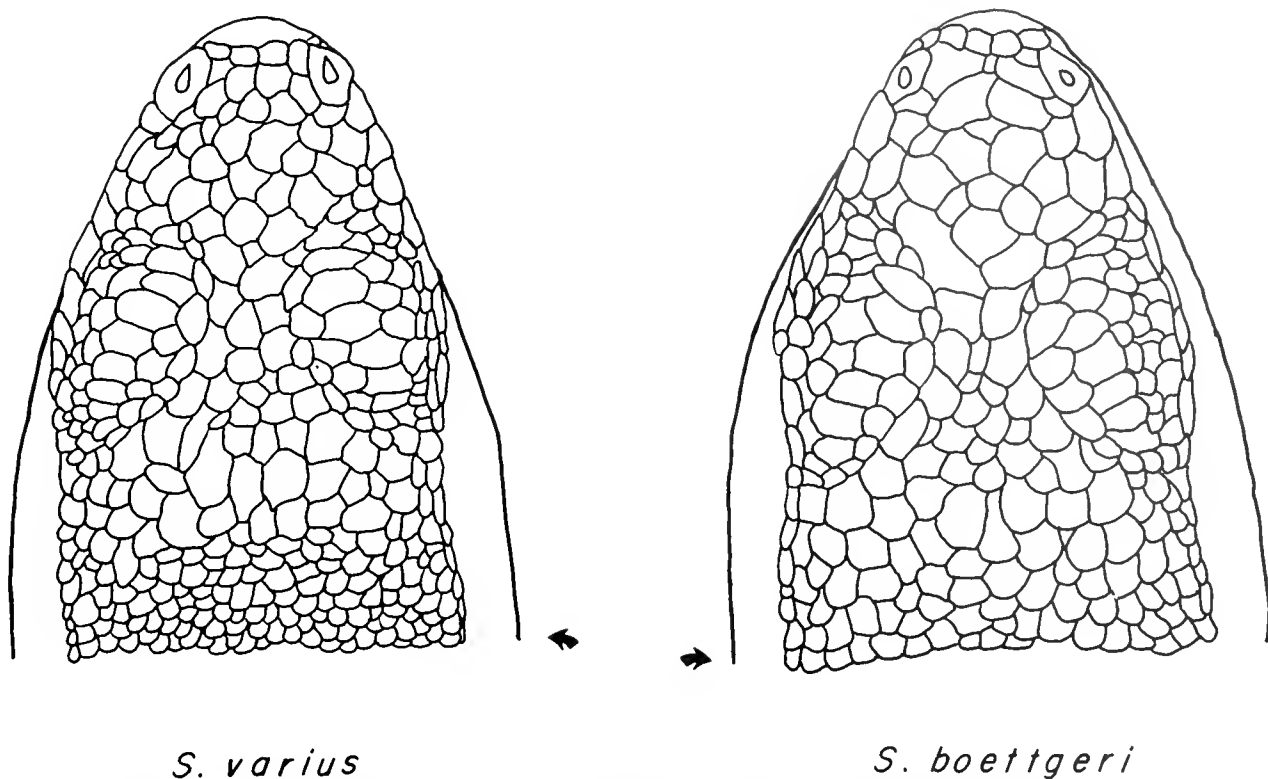


Figure 10. Dorsal cephalic scutellation of *Stenocercus boettgeri*, KU 134014, male, x 5. and *S. varius*, KU 132494, x 7. Arrows indicate anterior margin of tympanum.

and rock walls. The dorsal coloration of yellow flecks on a black ground color closely approximates the color of the dark rocks partially covered with yellow lichens on which the lizards occur near Paucartambo, Departamento Pasco. The lizards seek refuge in crevices within rock piles and are capable of inflating the lungs so as to wedge the body tightly in the irregular spaces between rocks. *Stenocercus boettgeri* and *S. nigromaculatus* likely occur in sympatry near Huancabamba, Departamento Piura, Perú. The latter species is largely confined to the ground and rows of *Agave*.

**Remarks.**— Little can be noted concerning the coloration of *S. boettgeri* in the northern populations. Boulenger (1911) presented the following notes: "Olive above with more or less indistinct darker cross bars". Boulenger did not see the specimens in life and probably was using preserved specimens for the basis of this description. Specimens from Paucartambo, 2900-3250 m, in central Perú, are black dorsally with numerous yellow flecks and

lines on the dorsal and lateral scales. Specimens from both central and northern Peru have a pinkish tint on ventral surfaces.

Etheridge (1970) considered *Stenocercus juninensis* Shreve (1941) to be synonymous with *S. boettgeri*. I have examined the type of *S. juninensis* (MCZ 45820) and find it to differ from *S. boettgeri* in having fewer dorsals in paravertebral row from head to base of tail 87, (90-113 in *S. boettgeri*); fewer scales across gular region between tympana 35, (43-55 in *S. boettgeri*) and fewer subdigital lamellae on fourth toe 21, (25-28 in *S. boettgeri*).

#### *Stenocercus carrioni* Parker

*Stenocercus carrioni* Parker, 1934:268.

Type Material.— BMNH 1933.6.24.75 (RR 1946.8.11.83) from Zamora, 3250 ft. Provincia Loja, Ecuador. The city of Zamora is presently included in Provincia Zamora, Ecuador.

**Diagnosis.**— 4) Scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales of posterior thigh granular; 6) vertebral row discontinu-

ous in some specimens, dorsal crest visible on neck only; 7) caudal scales large, extremely spinose, alternating large, small, large, small, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck folds present; 10) scales around middle of body 77-86.

Of the species of *Stenocercus* with 2 caudal whorls per autonomic segment only *S. carrioni*, *S. empetrus*, and *S. marmoratus* lack complete vertebral rows. *Stenocercus marmoratus* differs from the *S. carrioni* in possessing imbricate scales on the posterior thigh and fewer subdigital lamellae. *Stenocercus empetrus* differs in having caudal whorls which are subequal in size and in having a larger and more robust body. *Stenocercus carrioni* differs from *S. simonsii* in having caudal whorls markedly alternating in size; the smaller caudal scales are approximately one-half the size of the larger ones. The absence of a complete vertebral row is also distinctive in *S. carrioni* in comparison to *S. simonsii*.

*Distribution.*— Although the type specimen was reported from Zamora, Ecuador, on the Amazonian slopes, the only additional specimens are from the vicinity of Alamor, Provincia Loja, Ecuador, a locality in the Pacific drainage (Fig. 9) and adjacent regions of Provincia El Oro. The type was part of a collection given to the British Museum by Clodovo Carrion. Parker (1934) reported on many species in the Carrion collection; the report contains reference to several other species from "Zamora, 3250 ft.," which on the basis of present knowledge are doubted or known not to occur at the locality. Parker listed *Atelopus ignescens* from Zamora, although it is confined to higher elevations throughout the Andes of Ecuador; despite Parker's record from Zamora it is extremely doubtful that the Andean *Pholidobolus montium* occurs at elevations below 2000 m in southern Ecuador. I view the possibility of *Stenocercus carrioni* occurring on Amazonian slopes as slight. However communication between Atlantic and Pacific drainages through low passes in the Andes has been postulated for other species in southern Ecuador and

extreme northern Perú (Schmidt and Walker, 1943).

*Ecological Observations.*— *Stenocercus ornatus* and a species of *Ophryoessoides* are known from the environs of Alamor and are likely to be in sympatry with *S. carrioni*. On the basis of the phenetic similarity to many of the rock-dwelling species of the genus, *S. carrioni* is likely to confine its activity to rock outcrops and associated habitats.

*Stenocercus chrysopygus* Boulenger  
Fig. 23-24

*Stenocercus chrysopygus* Boulenger, 1900:183.

Type Material.— Syntypes BMNH 1900.6.20.8-17 (RR 1946.8.9.33-46) from Carao (Caraz), 8000 ft., BMNH 1900.6.20.18 (RR 1946.8.11.84) from Huaraz, 10,000 ft. and BMNH 1900.6.20.19 (RR 1946.8.5.98) from Recuay, 11,000 ft., Departamento Ancash, Perú. The type locality is herein restricted to Huaraz, 10,000 ft., Departamento Ancash, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket weakly developed; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales of posterior thighs granular; 6) vertebral row continuous or broken, not forming dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 54-82; 15) head scales smooth.

Of the species having granular scales on the lateral surface of the neck and lacking a distinct dorsal crest, only *Stenocercus chrysopygus* and *S. haenschi* lack a spinose tail. *Stenocercus chrysopygus* differs from *S. haenschi* in having fewer than 32 scales across the gular region between tympana, fewer than 23 subdigital lamellae on the fourth finger and in lacking green coloration. *Stenocercus chrysopygus* resembles *S. ornatus* in aspects of scutellation and body form, but differs from it in having a distinct postfemoral pocket, and granular scales on the lateral neck. It differs from *S. orientalis* in lacking keeled head scales and in having granular scales on the lateral neck.

*Distribution.*— This species is widespread on both sides of the Cordillera

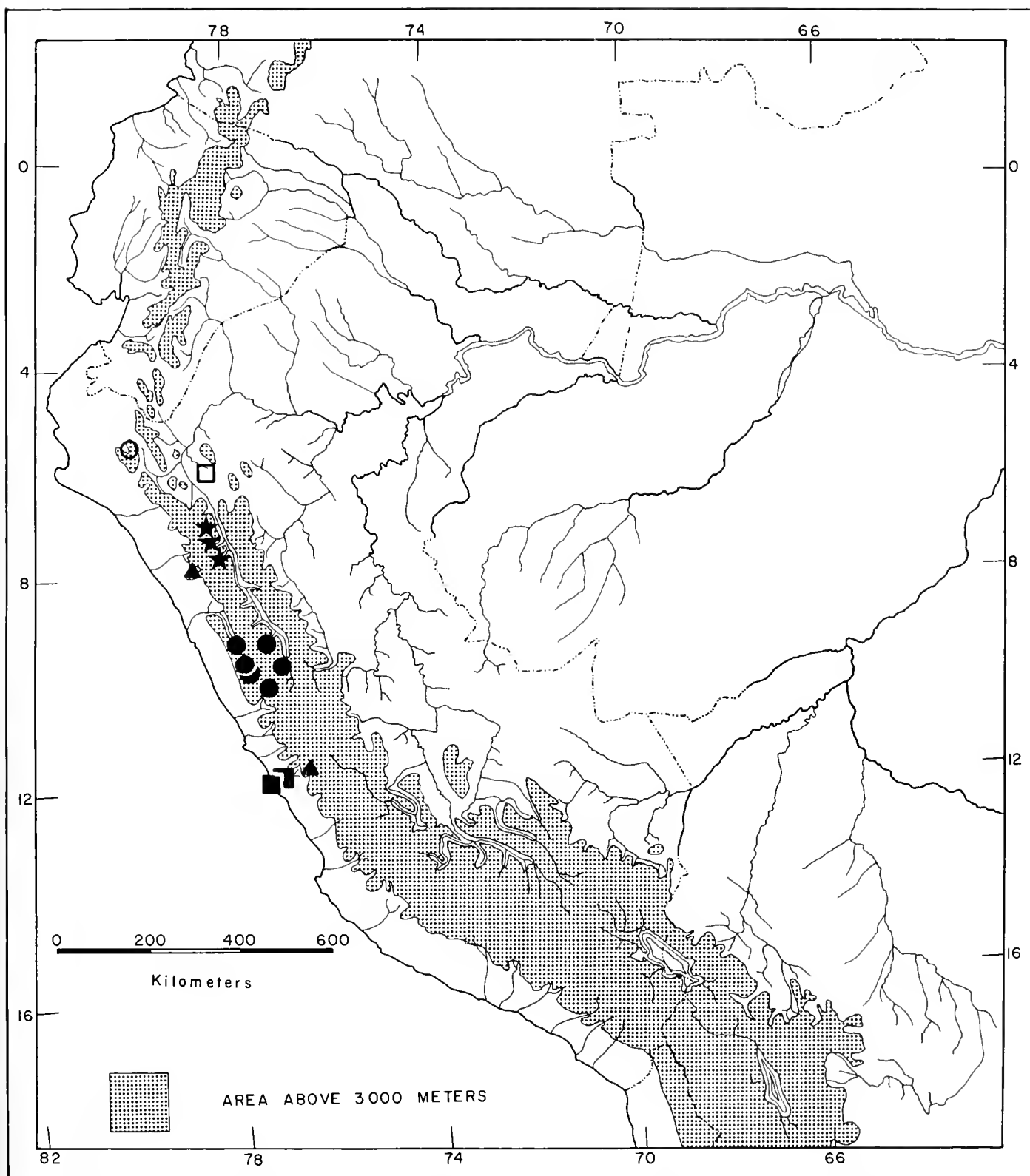


Figure 11. Distribution of *Stenocercus ivitus* (open circles), *S. chrysopygus* (closed circles), *S. orientalis* (open squares), *S. moestus* (closed squares), *S. ornatissimus* (triangles), *S. melanopygus* (stars) in the Andes of central and northern Peru.

Blanca of central Perú (Fig. 11). Populations are known in the upper reaches of the Río Chiquian and Río Santa on the Pacific slopes of the Departamento Ancash at elevations of 2265 to 3500 m. Populations are known in the Atlantic drainage from La Unión, 3100 m, Departamento Huánuco, and Chavin de Huantar, 3230-3500 m, Departamento Ancash. The Cordillera Blanca, the highest mountain range in Perú attains elevations of 4500-5000 m between the Atlantic and Pacific localities in this area of Perú.

The populations from Caraz, Huaraz, and Recuay are from different elevations of the Río Santa in the Departamento Ancash, and can be considered as a single panmictic unit. Chiquian is situated in the valley of the Río Chiquian to the south and is separated from the geographically close valley of the Río Santa by a ridge at 4300 m. Chavin de Huantar and La Unión are localities in different subvalleys of the Río Marañón.

*Ecological Observations.*— Males are most often observed on small rocks or mud walls. Females are found under rocks and at the bases of *Agave* and small shrubs. No other lizards are known to occur in sympatry with this species. A species of *Liolaemus* occurs at higher elevations between the valleys of the Río Santa and the Río Chiquian. Several species of *Tropidurus* are known from lower elevations on the Pacific slopes of this region.

*Remarks.*— The males of this species exhibit considerable variation in coloration within and between populations. Males from the valley of the Río Santa (Recuay, Huaraz, Caraz) have gray-white venters with dull yellow coloration on the ventral thighs and ventral pelvic region. An inverted yellow triangle on the ventral pelvic region is present in some males. The chin and gular region are light with a variable blue suffusion and prominent gray-black blotches. The ventrolateral body of some specimens is light to medium brown with a light blue suffusion. The gray-brown dorsolateral stripes are indistinctly defined on head and neck or are absent entirely.

Males from other localities (Chavin de Huantar, La Unión, and Chiquian) have

black coloration on the ventral pelvic region and thighs. The ventral base of the tail is yellow with black flecks or black in males from Chavin. The black ventral coloration extends anteriorly to the pectoral region. Some males from Chavin have a gray-black suffusion over a lighter ventral ground color. The chin and gular regions are light to medium blue with prominent black reticulations. Some specimens have a yellow or green suffusion on the apex of chin. The ventrolateral body is gray-blue to medium blue with black blotches. A prominent white or yellow stripe extends from the subocular region, passing dorsal to the tympanum, onto the shoulder. A short yellow or white stripe passes ventral to the tympanum from the subocular region to the base of the forelimb. These stripes are most distinct in males from La Unión and Chiquian.

Females from all localities are similar in coloration. Most individuals have gray dorsolateral stripes and two longitudinal series of irregular dark blotches on the dorsum. Females have a gray middorsal stripe without black flecks or blotches. The venter is beige-white with scattered gray flecks.

The populations studied are uniform in most aspects of the scutellation. The number of scales around the middle of the body and the number of transverse rows of dorsals from the head to the base of the tail vary geographically. These two characters are highly correlated and show similar patterns of variation. The Pacific populations (Chiquian, Huaraz, and Recuay) possess similar numbers of dorsal scales whereas the La Unión population possesses higher numbers and Chavin has the highest of all (Table 5).

Individuals from La Unión and Chiquian are markedly melanistic; lizards from Chavin are slightly melanistic but resemble lizards from Huaraz and Recuay in having the more typical dorsal coloration of terrestrial lizards of this genus. Lizards from La Unión have a continuous vertebral row of scales on the body whereas lizards from other localities seldom have a continuous vertebral row.

Table 5.

Basic statistics of five samples of *Stenocercus chrysopygus*. Vertical lines connect non-significant ( $p < 0.05$ ) subsets of SS-STP analysis.

Sample	N	$\bar{X}$	Range	SD	$2SE\bar{X}$	
Scales Around Middle of Body (SMB)						
Chavin	17	74.06	67-82	4.10	2.00	
La Union	10	65.80	59-70	3.16	2.00	
Recuay	37	60.59	55-68	3.20	1.05	
Huaraz	22	58.23	53-65	3.28	1.40	
Chiquian	15	58.07	54-62	2.46	1.27	
Scales Across Gular Region Between Tympana (SAG)						
La Union	10	28.20	25-31	2.00	1.26	
Chavin	17	27.65	25-30	1.62	0.78	
Recuay	37	25.54	23-29	1.63	0.53	
Chiquian	15	25.40	24-27	1.35	0.70	
Huaraz	22	24.64	21-28	1.47	0.62	

Because of the small number of samples available, few trends can be delimited with confidence. The two darkest color patterns occur in the most southern localities (Chiquian and La Unión); lizards from Pacific drainages have fewer scales around the middle of the body than do those from Atlantic populations.

*Stenocercus crassicaudatus* (Tschudi)

Fig. 28

*Scelotrema crassicaudatum* Tschudi, 1845:155.

Type Material.— Holotype MHNN unnumbered, from Perú; Tschudi (1846) further specified the type locality as Urubamba (Departamento Cuzco), Perú.

*Stenocercus torquatus* Boulenger, 1885:133.

Type Material.— BMNH 61.5.22.4 from Perú.

*Urocentrum meyeri* Werner, 1904:4.

Type Material.— The holotype (number unknown) was destroyed in the Dresden Museum during World War II. The type locality [cited as] Lima, Perú is probably erroneous.

*Stenocercus ervingi* Stejneger, 1913:545.

Type Material.— USNM 49550 from Huadquinia, 5000 ft. (Departamento Cuzco), Perú.

**Diagnosis.**— 3) Dorsal scales near vertebral row imbricate and keeled, those near dorsolateral region granular, lateral scales granular; 4) scales posterior to

tympanum granular; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming low dorsal crest; 7) caudal scales large and spinose, two caudal whorls per autonomic segment of tail; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 85-119; 11) scales across gular region between tympana 50-59; 12) subdigital lamellae of fourth finger 30-37.

*Stenocercus crassicaudatus* differs from all other species with spinose caudal scutellation in having more subdigital lamellae on the fourth finger, a dorsal coloration of dark gray with black spots, and usually having more scales around the body.

**Distribution.**— *Stenocercus crassicaudatus* is known from elevations of 1000-2500 m on Amazonian slopes of central and southern Perú (Fig. 12). On the basis of two specimens (UMMZ 68115) from Yungas de Cochabamba, Bolivia, the species is considered to extend into Amazonian Bolivia. Whether this species has a continuous distribution from north-central Perú south to Amazonian Bolivia or not cannot be ascertained at this time. Invasion of the

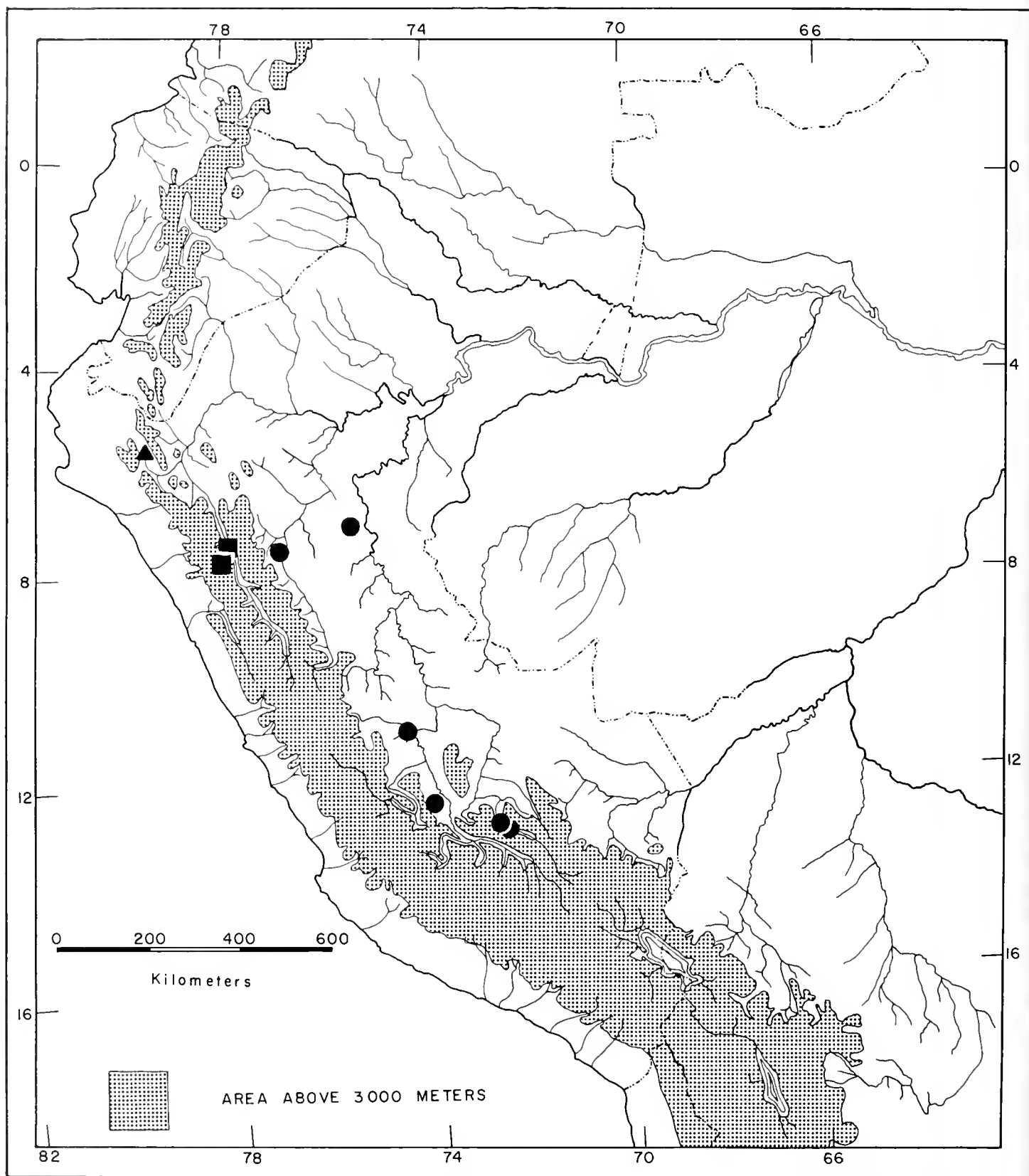


Figure 12. Distribution of *Stenocercus crassicaudatus* (circles), *S. empetrus* (squares) and *S. nigromaculatus* (triangles).

interandean valleys of Río Urubamba and Río Apurímac has been recorded to elevations of 2500 and 1400 m respectively (Mertens, 1952).

**Ecological Observations.**— *Stenocercus crassicaudatus* occurs on large rock piles and rocky cliffs at elevations of 1000 to 2500 m. *Stenocercus ochoai* occurs in sympatry with *S. crassicaudatus* between 2000 and 2500 m in the Río Urubamba valley. *Stenocercus ochoai* is confined to the ground, solitary rocks and small rock piles in areas of sympatry. Mertens (1952) recorded *Stenocercus crassicaudatus* and *Liocephalus arenarius* (*Stenocercus ochoai*?) in sympatry in the valley of the Río Apurímac: Aina, 1400 m, Departamento Ayacucho, Perú.

**Remarks.**— Specimens from Departamento Cuzco, Perú have numerous black spots on gray dorsal ground color on neck and body; those from Departamento Junín, Perú have a conspicuous black bar in the antehumeral region. The bar is occasionally complete across the dorsum forming a dorsal and lateral collar. One to three transverse black bars can be present on the neck. Specimens from central and southern Peru are similar in all scutellational attributes observed. Two specimens from Yungas de Cochabamba, Bolivia (UMMZ 68115) have fewer scales around the middle of the body (85 and 92) than any of the Peruvian specimens (more than 98 scales around body) of *Stenocercus crassicaudatus*.

*Stenocercus cupreus* Boulenger  
Fig. 33

*Stenocercus cupreus* Boulenger, 1885:135.

Type Material.— BMNH 76.7.4.4 from Huánuco, (Departamento Huánuco), Perú.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 3) dorsal scales keeled, twice as large as smallest laterals; 4) scales posterior to tympanum imbricate, one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, not forming distinct dorsal crest; 7) caudal scales large, not spinose, two caudal whorls

per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 52-64.

This is the only species having two whorls per autonomic segment and lacking spinose caudal scales. Of the species with two caudal whorls per autonomic segment, only *S. roseiventris* and *S. marmoratus* have as few scales around the body as *S. cupreus*. *Stenocercus cupreus* differs from *S. roseiventris* in lacking pink ventral coloration of males and granular scales on the posterior thigh, and differs from *S. marmoratus* in having a complete vertebral row and granular scales on the posterior thigh.

**Distribution.**— The species is known from the valley of the Río Huallaga, Departamento Huánuco, Peru between elevations of 1900 and 2300 m (Fig. 13). *Stenocercus chrysopygus* occurs in the adjacent upper Marañón Valley; one pass between the two valleys is at an elevation of 3900 m. *Liolaemus walkeri* is known to occur at elevations above 3400 m in the Nudo de Pasco, where the source waters of the Río Huallaga form.

**Ecological Observations.**— The vegetation of the xeric valley of the Río Huallaga consists of scattered cacti, grasses, and low shrubs. Males are observed basking on rocks, at bases of cacti and shrubs and rarely in the lowest branches of shrubs. Females are frequently at bases of shrubs and under rocks. There is little vegetation cover on the slopes of the valley; no other iguanids have been observed in sympatry.

*Stenocercus empetrus* Fritts  
Fig. 39-41

*Stenocercus empetrus* Fritts, 1972:7.

Type Material.— Holotype KU 134394 and paratypes KU 134379-134393, 134395-134400 from Huamachuco, 3350m, Departamento La Libertad, Perú.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket large; 3) dorsals imbricate, smooth or weakly keeled; 4) scales posterior to tympanum granular, smaller than dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row

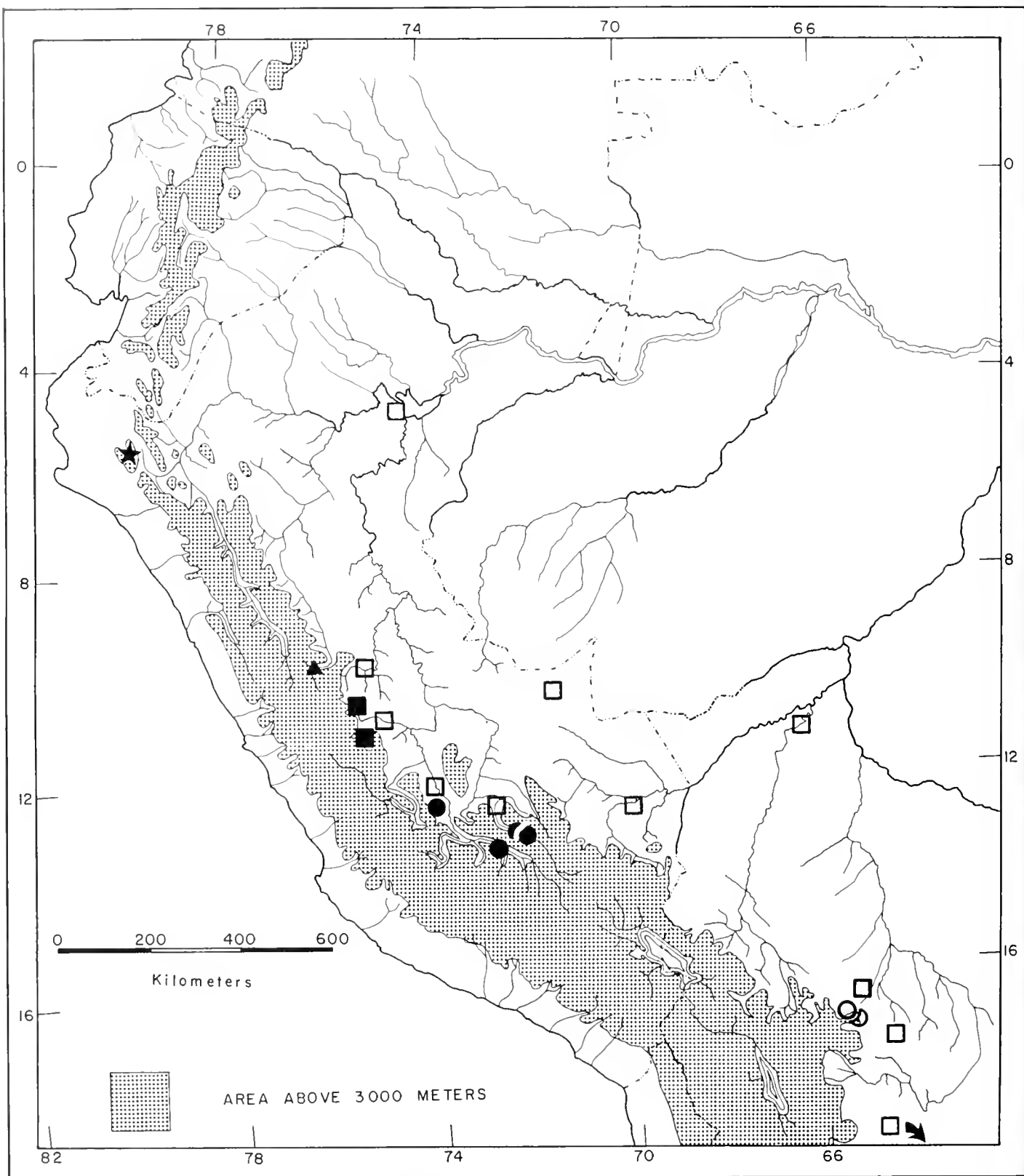


Figure 13. Distribution of *Stenocercus marmoratus* (open circles), *S. ochoai* (closed circles), *S. roseiventris* (open squares), *S. formosus* (closed squares), *S. cupreus* (triangles) and *S. nubicola* (stars).



discontinuous, only a few scales on neck and anterior body morphologically distinct from adjacent dorsal scales; 7) caudal scales spinose, enlarged, subequal, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold well-developed; 10) scales around middle of body 87-115; 11) scales across gular region between tympana 39-49; 13) dorsal body dark brown or black, numerous yellow flecks and spots on dorsum in some populations.

Three species of *Stenocercus* have spinose caudal scutellation and lack a continuous vertebral row. *Stenocercus empetrus* differs from *S. marmoratus* in having more than 86 scales around the middle of the body, more than 38 scales across the gular region between the tympana, and granular scales on the posterior thigh. *Stenocercus empetrus* differs from *S. carrioni* in having caudal whorls which are subequal in size and in having a more robust body. It differs from *S. simonsii* in lacking a vertebral row forming a distinct dorsal crest, in having smooth or weakly keeled dorsals, and in having a less spinose caudal scutellation.

*Distribution.*— The species is known from the valley of the Río Crisneja, adjacent tributaries of the Río Marañón, and a single locality in the Pacific drainage in the upper valley of the Río Moche (Fig. 12). It is distributed in the Peruvian departments of La Libertad and Cajamarca at elevations between 2650 m and 3200 m.

*Ecological Observations.*— Individuals of both sexes are saxicolous and occur in sympatry with the terrestrial species *Stenocercus melanopygus* in Atlantic localities. *Stenocercus empetrus* is likely sympatric with *S. ornatissimus* on Pacific slopes of north central Perú.

*Remarks.*— Considerable variation in dorsal coloration is evident (Fritts, 1972). Additional material is necessary for evaluation of morphological variation and relationships within the populations assigned to this taxon.

*Stenocercus festae* (Peracca) n. comb.

Fig. 37

*Liocephalus festae* Peracca, 1897:6.

Type Material.— Three syntypes MZT (numbers unknown) from Cuenca, (Provincia Azuay), Ecuador; none of the syntypes could be located in Turin by Richard Etheridge in 1967.

*Diagnosis.*— 1) Posthumeral pocket present; 2) postfemoral pocket well-developed; 3) lateral scales not greatly reduced in size in relation to dorsals; 4) scales posterior to tympanum nearly imbricate, keeled, equal in size to dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming raised dorsal crest; 7) caudals normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 47-60; 12) subdigital lamellae of fourth finger 16-22; 13) venter of males black; 14) gular region of males black.

*Stenocercus festae* differs from all other species lacking an antehumeral fold, in having a black blotch on the gular region of males, a black venter in males, smooth ventrals in adults, and a posthumeral pocket.

*Distribution.*— *Stenocercus festae* is known in Ecuador from throughout the Cuenca Basin (upper valley of Río Paute) and the adjacent Pacific slopes at elevations from 2300 to 2900 m (Fig. 14). The valleys of the Río Paute (Atlantic drainage) and Río Jubones (Pacific drainage) are separated by a ridge less than 3000 m in elevation. All localities are in the provinces of Canar, Azuay, Loja and El Oro.

*Ecological Observations.*— *Stenocercus festae* occurs in sympatry with *S. simonsii* in the upper Río Jubones drainage. In this area *S. festae* utilizes the leaves of agave plants and surrounding ground surface for basking and feeding activity, whereas *S. simonsii* is restricted to large rocks or rock piles. *Stenocercus rhodomelas* and *S. ornatus* are known from geographically proximal regions.

*Remarks.*— The juveniles of this species have weakly keeled ventrals, al-

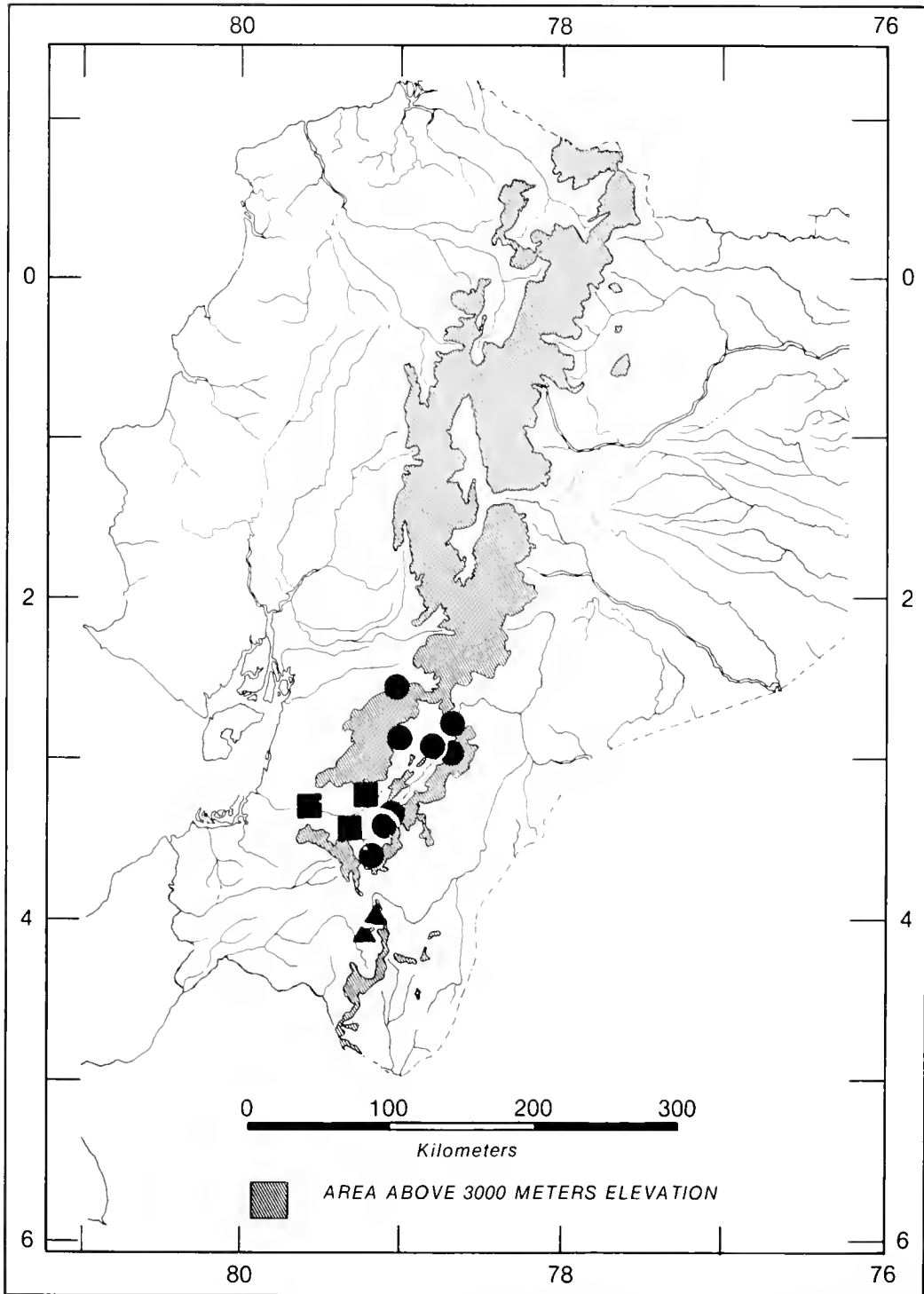


Figure 14. Distribution of *Stenocercus festae* (circles), *S. rhodomelas* (squares) and *S. ornatus* (triangles) in the southern Andes of Ecuador.

though no trace of keeling remains in sub-adults or adults. The ventral coloration is variable between geographically proximal localities. Male individuals from the valley floor at 2500 m near Cuenca have a light

yellow chin and lateral venter; some of those from 8 km NW Cuenca, 2620 m are similar whereas others have a solid black ventral surface from the snout to the vent. Males from SW of Cuenca near Cutchil,

2500-2900 m, Provincia Azuay, have a light orange coloration on the chin and pectoral region. No notes on the color of live specimens are available for adults from the Pacific slopes, although juveniles have light yellow coloration on the labial scales. Preserved specimens from the Pacific slopes retain the black coloration on the gular and ventral regions.

Specimens from Azogues, 2500 m, Provincia Canar, have more scales around the middle of body 59.3 and more scales across the gular region between tympana 28.5 than those from Cuenca, 2540 m, Provincia Azuay 50.9 and 24.7 respectively ( $p < 0.05$ ; SS-STP).

*Stenocercus formosus* (Tschudi) n. comb.

Fig. 31

*Scelotrema formosus* Tschudi, 1845:155.

Type Material.— Two unnumbered syntypes in MHNN from Perú; locality further specified by Tschudi (1846) as Tullumayo, Montañas des Mittlern Perú.

*Liocephalus rhodogaster* Boulenger, 1901:547. new synonymy.

Type Material.— BMNH 1900.11.27.24-25 (RR 1946.8.29.81-2) from La Merced, 3250 ft., Río Perene, (Departamento Junín), Perú.

*Liocephalus lineogularis* Werner, 1901:3. new synonymy.

Type Material.— D 1781 from Chanchamayo, (Departamento Junín), Perú; type destroyed during World War II.

*Stenocercus seydi* Andersson, 1908:301. new synonymy.

Type Material.— Single specimen WNM (number unknown) from La Merced, 1000m, (Departamento Junín), Perú.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket deep; 3) lateral scales nearly equal in size to dorsals; 4) scales posterior to tympanum imbricate, less than one-half size of dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming raised dorsal crest; 7) caudal scales normal, three or four caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around body 78-81; 11) scales across gular region between tympana 29-31; 13) venter of adult males pink with black midventral stripe.

Of the species having imbricate, keeled scales on the posterior surface of the thigh, only *S. formosus* and *S. ochoai* have antehumeral folds, neck folds and normal caudal scutellation. *Stenocercus formosus* differs from *S. ochoai* in having pink ventral coloration of adult males, in having more than 75 scales around the body and in having four caudal whorls per autonomic segment near the base of the tail.

**Distribution.**— *Stenocercus formosus* is known from the "Chanchamayo" region of Amazonian Perú (Fig. 13). The distribution extends from 1000 to 1600 m in the departments of Junín and Pasco. Previous workers (Burt and Burt, 1930; Mertens, 1952) have confused this species with *S. ochoai* from the valleys of the Río Apurímac and Río Urubamba in southern Perú. *Stenocercus formosus* is confined to the drainage of the headwaters of the Río Perene. *Stenocercus ochoai* occurs in the more southern valleys of the Río Urubamba and Río Apurímac and is not known to reach the Río Perene drainage. *Stenocercus formosus* occupies several small valleys on the eastern slopes of the Andes.

**Ecological Observations.**— Individuals are observed on the ground, in small shrubs and on small rock piles. They seek refuge in rock piles and holes around the base of shrubs. Montane tropical forest covers most of the geographic distribution of this species. No other *Stenocercus* species occurs in sympatry. *Stenocercus praeornatus*, *S. boettgeri*, and *S. variabilis* are known from higher elevations in the same region.

**Remarks.**— The trivial name of this species has been confused by all previous workers; *Steironotus arenarius* Tschudi (1845) was considered a senior synonym of *Liocephalus rhodogaster* by Roux (1907) and by subsequent workers. I have found *Steironotus arenarius* Tschudi to be a species of *Tropidurus* synonymous with *Tropidurus tschudi* Roux (1907). Evidence exists which indicates that Roux inadvertently used the type specimen of *Steironotus arenarius* Tschudi as the type specimen of *Tropidurus tschudii*. In the same bottle as

the specimen of *Tropidurus* named by Roux were two specimens which Roux considered to be the types of *Steironotus arenarius* and found to be conspecific with *Liocephalus rhodogaster* Boulenger (1901). The name *Scelotrema formosum* Tschudi (1845) has never been allocated by subsequent workers (Boulenger, 1885; Burt and Burt, 1933). Roux reviewed some of Tschudi's types but did not comment on *S. formosum* presumably because he did not find the type in the Neuchatel collection. Most authors have considered *S. formosum* likely to be allied to the "South American *Liocephalus*" *Ophryoessoides*, or *Stenocercus*. Boulenger (1885) listed *Scelotrema* in the synonymy of *Liocephalus* although he failed to allocate *S. formosum*, perhaps because of uncertainty and the homonymy that would result with *Liocephalus formosus* Boulenger (1880).

In studying Tschudi's original description (1845) and his redescription (1846) of *Scelotrema formosum*, I find that the characters discussed closely fit those of *Liocephalus rhodogaster* (Boulenger, 1901).

Most characteristics given by Tschudi are comparable with ones observed in a recently collected series of lizards from central Perú (Table 6). The illustration of *Scelotrema formosum* in Tschudi (1846, pl. 1, fig. 1), the description and the measurements indicate that Tschudi was in possession of a subadult or adult male, although the measurements do not agree with those of Roux (1907) and cannot be accepted with confidence. The illustration of the type, although of poor quality, is recognizable as a *Stenocercus* or *Ophryoessoides* on the basis of the coloration. *Scelotrema formosum* as described by Tschudi differs only in minor points from *Liocephalus rhodogaster*. *Scelotrema formosum* is said to lack pterygoid teeth; *L. rhodogaster* has 1 or 2 minute pterygoid teeth per side which are sometimes covered by the mucosa of the mouth. If Tschudi merely looked at the pterygoid region without probing in the mucosa, he could have overlooked the inconspicuous pterygoid teeth of this species. The white spots on the body of *S. formosum* are greenish white in

Table 6.

Comparison of *Steironotus arenarius* Tschudi, *Scelotrema formosum* Tschudi and *Liocephalus rhodogaster* Boulenger. Data from Tschudi (1846) and Boulenger (1901). The description of the last species is supplemented by a recent series of lizards (KU 134109-134113).

Characters	<i>Steironotus arenarius</i>	<i>Scelotrema formosum</i>	<i>Liocephalus rhodogaster</i>
Interparietal	large	small	small
Gular fold	present	absent	absent
Parietals	"large"	?	small
Lateral venter	green with black spots	violet	violet
Chin of males	light	pink	pink
Shoulder	5 transverse dark blotches	light stripe	light stripe
Postfemoral pocket	weak	deep	deep
Scales of ventral pectoral region in relation to ventrals	larger	equal	equal
Suborbital stripe	?	prominent	prominent
Pterygoid teeth	4-6	0	1-2

life in *L. rhodogaster*. Tschudi referred to the cinammon-brown dorsum with red on the posterior margin of each scale; specimens of *L. rhodogaster* are various shades of brown with some males having a reddish suffusion which is most conspicuous on the lateral body. The dark dorsal blotches of *L. rhodogaster* are often outlined with white or yellow whereas those of the type of *S. formosum* are said to be outlined with yellow. The lateral body of males of *L. rhodogaster* is brown, slightly darker than the dorsal head whereas it is dull black in females. Tschudi's reference to a velvet black lateral head may be a result of discoloration of the specimen in alcohol, or the use of both sexes in compiling the description. Tschudi's statements referring to a violet ventral coloration and a pink chin indicate that he had a male. Roux (1907) indicated the presence of three specimens in a jar labeled *Steironotus arenarius* in the Neuchâtel museum. Roux concluded erroneously that the two specimens similar to *L. rhodogaster* represented the types of *Steironotus arenarium* and that the third specimen was an undescribed *Tropidurus*; in fact the two specimens similar to *L. rhodogaster* were the types of *Scelotrema formosum* and the specimen of the "new" species of *Tropidurus* was the type of *Steironotus arenarius*. Roux's work despite his erroneous conclusions does indicate that more than one specimen of *Scelotrema formosum* was available to Tschudi and facilitates understanding of the reference to characteristics of both sexes in the description (Tschudi, 1846).

The midventral stripe of males of *L. rhodogaster* is absent in juveniles, gray in subadults and black in adults. Tschudi referred to a yellow-green midventral stripe. *Liocephalus rhodogaster* has conspicuous dark transverse markings on the tail; *S. formosum* was described as having dark transverse markings with yellow centers.

Except for the differences noted, the morphology described for *Scelotrema formosum* Tschudi agrees with that of *Liocephalus rhodogaster* Boulenger. Dr. Richard Etheridge (pers. comm.) examined the

specimens assumed by Roux to be types of *Steironotus arenarius* but here shown to be the types of *Scelotrema formosum*; Etheridge found the cotypes to agree with the type of *Liocephalus rhodogaster* which he had examined previously in the British Museum (Natural History).

On the basis of the original descriptions and subsequent discussions of the two taxa, I consider *Liocephalus rhodogaster* Boulenger to be a junior synonym of *Scelotrema formosum*. *Scelotrema formosum* is assigned to the genus *Stenocercus* on the basis of the morphology which compares well with other species and the present diagnosis of the genus.

The type locality of *Stenocercus formosus* given by Tschudi (1847) of "Montañas des mittlern Perú: am Tulumayo" probably refers to the Río Tulumayo, Departamento Junín, a tributary of the Río Perene. Most of the Río Tulumayo is within the range of specimens previously assigned to *L. rhodogaster*. It is a moot point to argue further whether the specimens examined by Roux and Etheridge and found to be identical with *Liocephalus rhodogaster* were the types of *Scelotrema formosum*.

The recognition of *Scelotrema formosum* Tschudi as a *Stenocercus* creates secondary homonymy with *Liocephalus formosus* Boulenger (1880), which is also a member of the genus *Stenocercus*. Replacement of the name *Liocephalus formosus* Boulenger (1880) with an available junior synonym is necessary. See the species account of *Stenocercus haenschi* Werner (1901).

Among the characteristics listed by Andersson (1908) for *Stenocercus seydi* are several which indicate that a specimen of *Stenocercus formosus* was being described. Andersson described a repeating sequence of 4 caudal whorls (per autonomic segment); *S. formosus* is the only species in the genus with more than 3 caudal whorls per autonomic segment. The aspects of scutellation and coloration mentioned by Andersson agree with those known in *S. formosus* and prompt synonymy of the two taxa.

*Stenocercus guentheri* (Boulenger) n. comb.  
Fig. 19-21

*Liocephalus guentheri* Boulenger, 1885:169.

Type Material.— Syntypes BMNH 58.7.25.16, 58.7.25.18, 60.6.16.18-21, 80.12.8.53, 59.9.20.b, 71.4.16.53(9), 71.2.7.7-10 from Guayaquil (Provincia Guayas), Ecuador; Sarayacu (Provincia Pastaza), Ecuador; and an unspecified locality in Colombia. *Stenocercus guentheri* occurs at none of the localities given for the type material. The presence of a black gular patch on at least one of the male syntypes indicates that it was collected in the Pichincha Basin of Ecuador; the type locality is herein restricted to San Antonio de Pichincha, 2500m, Provincia Pichincha, Ecuador.

**Diagnosis.**— 1) Posthumeral pocket absent or only weakly developed; 2) postfemoral pocket present, variable in size; 3) lateral scales not greatly reduced in size in relation to dorsal scales; 4) scales posterior to tympanum imbricate, keeled, nearly equal in size to dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming raised dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 58-89; 11) scales across gular region between tympana 25-38; 13) venter of males variable in coloration; 14) chin of males not black.

*Stenocercus guentheri* differs from all species lacking antehumeral and neck folds except *S. apurimacus* in usually having more than 60 scales around the midbody, and more than 24 scales across the gular region between tympana. It differs from *S. apurimacus* in lacking a deep posthumeral pocket, large scales which are wider than long in the occipital region, and in having a postfemoral pocket.

**Distribution.**— *Stenocercus guentheri* is the most widely distributed species of the genus in Ecuador, where it extends from Imbabura Province southward to Azuay Province (Fig. 9). It occurs altitudinally from 2100 m to 3890 m. Most localities are from the slopes of the interandean valleys between the two principal Andean cordilleras; both Pacific and Atlantic drainages are inhabited.

**Ecological Observations.**— *Stenocercus*

*guentheri* is not known in sympatry with other *Stenocercus*. Males tend to bask and search for food on rocks and other elevated positions, whereas females are most commonly noted feeding on the ground. At localities where exposed rocks and rock walls are uncommon, individuals of both sexes seek refuge in holes in the ground at the bases of plants (*Agave*, *Stipa*, and others).

One female (KU 134474) was observed covering a small hole containing two eggs near Guamate, Chimborazo Province, on 11 June 1970. Eighteen females collected near Mulalo, Provincia Cotopaxi deposited two eggs each in the laboratory between 16 May and 18 June 1972.

**Remarks.**— *Stenocercus guentheri* remains taxonomically bewildering in exhibiting several divergent morphological types including considerable geographic variation. A detailed study of variation within the species is underway. However, present knowledge precludes all but a superficial discussion of variation. Males from the Imbabura and Pichincha basins have a narrow yellow midventral stripe with lateral areas of venter gray-blue to greenish gray; males from the Central Valley (Cotopaxi and Chimborazo basins) have yellow venters with numerous dark spots. The population from Alausí, Provincia Chimborazo, south of the southern margin of the central valley includes males with red-orange venters, others with light yellow venters and additional individuals with blue-green ventral fields separated by a black midventral stripe. Males from the Pichincha Basin have black patches on the gular region similar to those of *Stenocercus festae*; males from other valleys lack such black markings.

The number of scales around the middle of the body is higher in some populations in the Central Valley than in those in the Imbabura and Pichincha Basins. This possibly reflects a greater range of variation within the Central Valley rather than a distinct geographic trend. Three local populations from the Imbabura Basin have means of 64.0 to 68.1; three populations

from the Pichincha Basin have means of 64.2 to 68.0. Nine populations from the Central Valley have means of 66.1 to 77.2. Means for the two populations south of the Central Valley, Alausí, Provincia Chimborazo, and Sevilla de Oro, Provincia Azuay, are 67.2 and 62.1 respectively.

A similar pattern of greater variability of populational means in the Central Valley can be seen in the number of scales from occiput to rostral. The ranges of the means for the Imbabura Basin, Pichincha Basin and Central Valley are 15.0 to 16.8, 15.1 to 15.7 and 16.0 to 18.4 respectively. The samples from Alausí and Sevilla de Oro have means of 17.9 and 17.1 respectively. The extent of sexual dimorphism in size and color pattern remains to be fully investigated. Field observations suggest that increased structural diversity in habitat (*i.e.* large patches of rock similar to the lava fields at Lago Cuicocha, Provincia Imbabura, and rock-shrub habitat near Alausí, Provincia Chimborazo) is accompanied by greater sexual dimorphism and increased variability. The absence of patchy resources or low density and small size of such patches can limit sympatric occurrence of ecologically similar species (Levins, 1968). The absence of structural diversity in habitat (*i.e.* the scarcity of exposed rocks in the northern Ecuadorian Andes) is a possible explanation of the allopatric distribution of *S. guentheri*. The distribution of Pleistocene volcanism in Ecuador, as mapped by Saur (1957), closely approximates that of *Stenocercus guentheri*. The rapid weathering of certain volcanic products possibly explains the absence of extensive areas of exposed rock and the absence of a completely saxicolous lizard in sympatry with *S. guentheri*. Where heterogeneous habitat patches do exist locally, morphological adaptation by one or both sexes within the limits of genetic plasticity available is likely. Such an hypothesis would explain the extreme inter- and intrapopulational variation known in *S. guentheri*.

*Stenocercus haenschii* (Werner) n. comb.

*Liocephalus formosus* Boulenger, 1880:43. A junior secondary homonym of *Scelotrema formosum* Tschudi (1845) = *Stenocercus formosus* (Tschudi).

Type Material.— BIN 2007 from Andes del Equateur; the type locality is herein restricted to Balzapampa, Provincia Bolivar, Ecuador.

*Liocephalus haenschii* Werner, 1901:595.

Type Material.— ZMB 16595 from Balzapampa, 750m, (Provincia Bolivar), Ecuador.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket absent; 3) dorsal scales imbricate, keeled; 4) scales posterior to tympanum imbricate and keeled, one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, not modified into dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around body 57-62; 11) scales across gular region small, approximately 40; 15) head scales smooth.

The blue-green coloration noted by Boulenger and Werner in the two known specimens of *S. haenschii* is approximated in only two other species—*S. varius* and *S. humeralis*. Both differ from *S. haenschii* in having more scales around the body, more cephalic scales between rostral and occiput, and a distinct vertebral crest.

**Distribution.**— The species is known from two specimens which are the types of *Leiocephalus haenschii* Werner and *Leiocephalus formosus* Boulenger, respectively. The former was reported from Balzapampa [Provincia Bolivar], Ecuador; the latter from the Andes of Ecuador (Fig. 9). The town of Balzapampa at 800 m elevation lies at the base of the major range of the Cordillera Occidental. The locality "Balzapampa" possibly includes a great range of elevations, above 800 m, within a close geographic proximity to the town.

**Ecological Observations.**— Little is known concerning this species. The green dorsal coloration and high number of subdigital lamellae of the fourth finger (26-28) indicate that *Stenocercus haenschii* is likely an arboreal species. Both *S. humeralis* and



*S. varius* have green dorsal coloration and are arboreal. All other species of the genus having a high number of subdigital lamellae of the fourth toe occupy arboreal or rock habitats.

*Remarks.*— The status of the two names, presently considered synonyms of *Stenocercus haenschi*, remains doubtful since their publication over 70 years ago. Examination of the type specimens of both species has revealed close similarity in morphology necessitating the present synonymy. Both specimens are clearly members of the genus *Stenocercus*.

### *Stenocercus humeralis* (Günther)

*Microphractus humeralis* Günther, 1859a:90.

Type Material.— BMNH (RR 1946.8.11.76-77) from Andes of Ecuador; the type locality is herein restricted to Loja, 2150m, Provincia Loja, Ecuador.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 3) dorsal scales near vertebral row imbricate, keeled; dorsals more laterally positioned granular, small, dorsals grading into small, granular lateral scales; 4) scales posterior to tympanum granular, less than one-half the size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming low dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around body more than 99; 11) scales across gular region between tympana more than 36; 13) dorsal coloration green.

*Stenocercus humeralis* differs from the other species with green coloration, *S. haenschi* and *S. varius*, in having more scales around the body and more subdigital lamellae on the fourth finger.

*Distribution.*— *Stenocercus humeralis* is known from southern regions of Ecuador in Loja Province in the upper Río Catamayo (Pacific drainage) and Río Zamora (Atlantic drainage) at elevations of 2000-3000 m (Fig. 9). In its lowest areas the continental divide in Loja Province is approximately

2700 m in altitude.

*Ecological Observations.*— Near the city of Loja at 2150 m *Stenocercus humeralis* is abundant only in specific habitats. Individuals occur in small shrubs and on the trunks of eucalyptus trees in mesic quebradas as well as in agave plants on top of earth fences. *Stenocercus ornatus* occurs in sympatry in the upper Río Zamora Valley; the latter species is confined to more open habitats at bases of shrubs and in low agave rows. *Stenocercus festae* possibly occurs in sympatry with *S. humeralis* on the Pacific slopes.

### *Stenocercus ivitus* Fritts

*Stenocercus ivitus* Fritts, 1972:10.

Type Material.— Holotype KU 134654 from summit of Cordillera Huancabamba between Canchaque and Huancabamba, 3100m, Departamento Piura, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum imbricate, keeled, nearly equal in size to dorsal neck scales; 5) scales of posterior thigh granular; 6) vertebral row discontinuous, vertebral scales not forming dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 44.

*Stenocercus ivitus* differs from all other species lacking antehumeral folds and neck folds in lacking a continuous vertebral row which forms a dorsal crest and in having granular scales on the posterior surface of the thigh.

*Distribution.*— *Stenocercus ivitus* is known only from the type locality at the summit of the Cordillera Huancabamba (Fig. 11). This cordillera forms the continental divide between the Río Piura (Pacific drainage) and the Río Huancabamba (Atlantic drainage).

*Ecological Observations.*— The adult female was observed basking on a pile of dead branches at the margin of a low shrub forest, and in sympatry with *S. nubicola*.



*Stenocercus marmoratus* (D'Orbigny)

*Trachycyclus marmoratus* D'Orbigny, 1837, in, Duméril and Bibron, 1837:356.

Type Material.— MHNP 2513 from Río Grande, Brazil; in error.

*Stenocercus difficilis* Werner, 1910:23.

Type Material.— Holotype ZMH (number unknown) from Cochabamba (Departamento Cochabamba), Bolivia.

**Diagnosis.**— 3) Dorsals imbricate, keeled; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales on posterior thigh imbricate, keeled or smooth; 6) vertebral row rarely complete, vertebral scales not distinctly modified from other dorsal scales; 7) caudal scales large, with prominent keels, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 43-54.

This is the only spiny-tailed *Stenocercus* with a discontinuous vertebral row and imbricate scales on posterior thighs.

**Distribution.**— *Stenocercus marmoratus* is known from Andean slopes between 2700 and 3350 m in the Departamento Cochabamba, Bolivia (Fig. 13). *Stenocercus marmoratus* occupies the highest elevations of any of the southern species of *Stenocercus*.

**Ecological Observations.**— A species of *Liolaemus* similar to *L. alticolor* is known from similar elevations within the range of *Stenocercus marmoratus*; the two species possibly occur in sympatry. The *Liolaemus* is small and exhibits a morphology similar to ground-dwelling species of *Stenocercus* and other *Liolaemus*, whereas *Stenocercus marmoratus* possesses a spinose tail and lacks a high dorsal crest similar to rock-dwelling species of *Stenocercus*. The *Liolaemus* occurs on the ground and at the bases of clump grasses. No field observations are available for *Stenocercus marmoratus*.

**Remarks.**— Duméril and Bibron (1837) cite D'Orbigny "Voy Amer. mer. Zoolog. Rept. tab. 4, fig. 2. (non encore publie.)" as the author of the name. D'Orbigny (1847)

later published his work.

Duméril and Bibron (1837) were cited as the authors of the name *Trachycyclus marmoratus* by Burt and Burt (1933) and by Etheridge (1970). The interpretations of authorship described in the International Code of Zoological Nomenclature (1964: art. 50-51) clearly provide for authorship by an author in the work of another author or other authors if such responsibility "is clear from the contents of the publication. . ." The citation of plates in D'Orbigny's then unpublished work and the failure to place "Nobis" behind the name both imply that Duméril and Bibron considered D'Orbigny responsible for the proposal of the name *Trachycyclus marmoratus*.

*Stenocercus melanopygus* Boulenger

Fig. 26

*Stenocercus melanopygus* Boulenger, 1900:182.

Type Material.— Syntypes BMNH 1900.3.30.6-9 (RR 1946.8.11.85-88), 1900.3.30.10-13 (RR 1946.8.11.78-81) from Baños, 9000 ft. (Departamento) Cajamarca, Perú.

**Diagnosis.**— 4) Scales posterior to tympanum imbricate, keeled, nearly equal in size to those of dorsal neck; 5) scales on posterior thigh granular; 6) vertebral row discontinuous, no dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold absent; 10) scales around middle of body 44-58.

*Stenocercus melanopygus* and *S. nigromaculatus*, are the only species in the genus which have antehumeral folds, but lack neck folds and posthumeral pockets. *Stenocercus melanopygus* differs from *S. nigromaculatus* in lacking a continuous vertebral row and high dorsal crest. Some individuals of *Stenocercus moestus* seemingly lack neck folds and have only small patches of granular or small imbricate scales in the approximate position of the neck folds. *Stenocercus moestus* differs from *S. melanopygus* in having less than 40 scales around the middle of the body.

**Distribution.**— The species is known at elevations of 2700-3250 m in the interandean valleys in the Peruvian departments of

Cajamarca and La Libertad (Fig. 11). All localities except Celendin are within the drainage of the Río Crisnejas. Celendin lies in an adjacent valley separated from the Río Crisnejas drainage by a ridge approximately 3300 m in elevation. The species is likely widespread in the western tributaries of the Río Marañón.

The species is not known from Pacific drainages, although the distribution occupies the most western parts of the Amazonian drainage in north-central Perú. The western slopes of the Río Marañón Valley are broken only by minor ridges into east-west rivers feeding into the Río Marañón. The major physiographic features which correlate with the limits of the distribution of this species are the low elevations and dry conditions prevalent in the area of the Abra Porculla in the north, the Sierra Occidental on the west, and the low elevation of the Río Marañón Valley on the east.

*Ecological Observations.*— *Stenocercus melanopygus* occurs in sympatry with *Stenocercus empetrus*. The former species utilizes the ground, blades of agave plants, solitary rocks, and the extreme edges of large rock piles for basking and feeding activity, whereas the latter species inhabits large rock piles, rock cliffs and rock exposures. Localities where *S. melanopygus* occurs are moist and support moderate vegetation for this region. On a local basis, specimens are more common on dry hillsides where rocks are scattered, and vegetation is sparse; in moist areas on the valley floor or on gentle slopes, both species are found together in proportions seemingly correlated with their respective habitat preferences.

Near Cajamarca, 2800 m, Departamento Cajamarca, Perú, *S. empetrus* is rare on extremely dry hillsides. Individual males of *S. melanopygus* occupy large rock piles and rock exposures which are usually utilized by *S. empetrus* in areas of sympatry. The males of *S. melanopygus* in this area are larger (SVL 54-76 mm) than males from near Huamachuco (SVL 50-64 mm). The males from the vicinity of Cajamarca have a

color pattern differing from those from other localities and resembling the sympatric congener *S. empetrus*. The increase in size of males and their possession of a color pattern similar to rock-dwelling species probably facilitates exploitation of rock habitats in the local area where *S. empetrus* is rare. Possibly, populations considered to be *Stenocercus melanopygus* from other localities are specifically distinct from the lizards from Cajamarca; further knowledge of geographic variation, ecology and behavior is needed for understanding the variation within this species.

*Remarks.*— The most conspicuous variation in *Stenocercus melanopygus* is in size and coloration of males. Specimens from Cajamarca show more marked sexual dimorphism in size than those from other populations. The males from Cajamarca differ from those of other areas in having a black ventral pelvic region and ventral thighs instead of the yellow coloration present in other populations.

### *Stenocercus moestus* Boulenger

*Stenocercus moestus* Boulenger, 1885:136.

Type Material.— BMNH 75.2.13.3 from Lima (Departamento Lima), Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket weak; 4) scales posterior to tympanum imbricate, usually keeled, nearly equal in size to dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row discontinuous, no dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold weak or absent; 10) scales around middle of body 33-38.

*Stenocercus moestus* resembles *S. melanopygus* and *S. ivitus* in having extremely large scales on the lateral surface of the neck, but differs in usually having a weak neck fold. *Stenocercus moestus* also differs from *S. melanopygus* in having less than 40 scales around the middle of the body and from *S. ivitus* in having an antehumeral fold.

*Distribution.*— The species is known only from the valley of the Río Rimac near Lima, Departamento Lima, Perú (Fig. 11), from sea level to 762 m (Etheridge, 1970). The Río Rimac is one of the major rivers of the central Peruvian coast. The Abra Teclio, 4815 m in the upper Río Rimac is one of the lowest passes to Atlantic drainages at this latitude.

*Ecological Observations.*— I have not observed this species in the field. The valley of the Río Rimac is xeric with little natural vegetation. The extensive irrigation of the valley for agricultural practices has left only the rock and sand slopes and cliffs unmolested. Species of *Tropidurus* occur throughout the range of *Stenocercus moestus*. *Stenocercus ornatissimus* is known to occur at higher elevations, 3340 m of the Río Rimac, and possibly replaces *Stenocercus moestus* at intermediate elevations. The presence of a *Stenocercus* at low elevations of coastal Perú only in the valley of the Río Rimac is puzzling. Whereas other *Stenocercus* are known from Pacific drainages of Perú, all occupy elevations of 1500 m or higher.

*Stenocercus nigromaculatus* Noble  
Fig. 18

*Stenocercus nigromaculatus* Noble, 1924:112.

Type Material.— Holotype MCZ 17975 and paratypes MCZ 18766-18769 from Huancabamba, Province of (Departamento) Piura, Perú.

*Diagnosis.*— 1) Weak depression in axillary region, posthumeral pocket absent; 2) postfemoral pocket large; 4) scales posterior to tympanum imbricate, keeled, nearly equal in size to dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming high dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold distinct; 9) neck fold absent; 10) scales around middle of body 48-56; 11) scales across gular region between tympana 21-25; 13) venter of males with midventral black stripe bifurcating anteriorly at pectoral girdle, bifurcating posteriorly onto ventral surfaces of thighs,

lateral venter light bronze; 14) chin and gular region white with faint gray reticulation.

*Stenocercus nigromaculatus* most closely resembles *S. ornatus* and *S. rhodomelas*, from which it differs in having a strong antehumeral fold, and in lacking bright pink or red on ventral surfaces of males.

*Distribution.*— The species is known from the vicinities of Huancabamba and Chumaya, Departamento Piura, Perú (Fig. 12). I have observed individuals from 1900 to 2300 m in the valley of the Río Huancabamba. The specimens that Burt and Burt (1931) reported from Wavepongo [= Llavepongo], Ecuador are identifiable as *Stenocercus guentheri*; *Stenocercus nigromaculatus* is not known from Ecuador. The Río Huancabamba, a northern tributary of the Río Marañón, is separated from coastal regions by the Cordillera Huancabamba with passes as low as 2790 m and 3100 m. The Río Marañón Valley at this latitude has an elevation of 500 m and possibly limits the species on the east.

*Ecological Observations.*— Individuals of *Stenocercus nigromaculatus* bask and forage in rows of *Agave* and around bases of shrubs. Juveniles enter holes at the bases of small shrubs to avoid capture. The slopes of the valley have small shrubs, and extensive grass and shrub cover; few rocks are exposed. *Stenocercus boettgeri* was reported from Huancabamba by Boulenger (1911); additional specimens were collected near Huancabamba by Noble. I did not observe *S. boettgeri* in this region. *Stenocercus nubicola* and *S. ivitus* are known to occur at 3100 m in the Cordillera Huancabamba. *Tropidurus stolzmanni* and an unnamed species of *Ophryoscoptes* are known from lower elevations of the Río Huancabamba.

*Stenocercus nubicola* Fritts  
Fig. 16

*Stenocercus nubicola* Fritts, 1972:11.

Type Material.— Holotype KU 134107 and paratype KU 134108 from summit of Cordillera Huancabamba between Canchaque and Huancabamba, 3100m, Departamento Piura, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum imbricate and smooth or granular, less than one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row complete, forming dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold distinct; 9) neck fold present; 10) scales around middle of body 93-94; 11) scales across gular region between tympana 38-39; 13) black midventral stripe in males, bifurcate anteriorly, extending onto ventral thighs posteriorly. Of the species of *Stenocercus* having black pigment extending from the pelvic to pectoral girdle on the venter of males, only *S. nubicola* has more than 85 scales around the middle of the body.

*Stenocercus nubicola* closely resembles the geographically adjacent species, *S. nigromaculatus* in coloration, but differs from it in having a neck fold, granular scales on posterior thigh and more scales around the body.

*Distribution.*— *Stenocercus nubicola* is known only from the type locality (Fig. 13). The Cordillera Huancabamba forms the continental divide in extreme northern Perú and separates the Río Huancabamba Valley (Atlantic drainage) and the Río Piura Valley (Pacific drainage).

*Ecological Observations.*— *Stenocercus nubicola* occurs in sympatry with *Stenocercus ivitus*, in montane moist forest. *Stenocercus nigromaculatus* is known at lower elevations in the same region.

*Stenocercus ochoai* Fritts  
Fig. 32

*Stenocercus ochoai* Fritts, 1972:13.

Type Material.— Holotype KU 133888 and paratypes KU 133874-133887, 133889, 139263 from Chilca, 10 km NW Ollantaytambo, 2700m, Departamento Cuzco, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket deep; 3) dorsal scales imbricate, keeled, but slightly larger than lateral scales; 4) scales posterior to tympanum imbricate, usually keeled,

one-half size of dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming raised dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 57-67; 11) scales across gular region between tympana 19-26; 13) venter of adult males black.

*Stenocercus ochoai* is most similar to *Stenocercus formosus* (Tschudi) from which it differs in having fewer scales around the middle of the body, the entire ventral coloration of males black and three caudal whorls per autonomic segment.

*Distribution.*— *Stenocercus ochoai* (Fig. 13) is known between 2000 and 3000 m in the valleys of the Río Urubamba (Burt and Burt, 1930) and Río Apurimac (Mertens, 1952).

*Ecological Observations.*— *Stenocercus ochoai* occurs in sympatry with *Stenocercus crassicaudatus* between 2000 m and 2600 m in the Río Urubamba Valley, and with *Stenocercus apurimacus* at Curahuasi, 2700 m, Departamento Apurimac, in the Río Apurimac Valley. The species uses both ground and rock substrates.

*Stenocercus orientalis* Fritts  
Fig. 15

*Stenocercus orientalis* Fritts, 1972:14.

Type Material.— Holotype KU 134466 and paratypes 134447-134465, 134467-134473 from Chachapoyas, 2340m, Departamento Amazonas, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum imbricate, keeled, one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, not forming dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around the middle of the body 47-58; 15) head scales prominently keeled.

*Stenocercus orientalis*, *S. ornatissimus*, *S. moestus*, *S. haenschii* and *S. chrysopygus* differ from other species of *Stenocercus* in

lacking a dorsal crest and spinose caudal scutellation, and in having antehumeral and neck folds. *Stenocercus orientalis* is the only one of these having prominently keeled scales on the snout and interorbital region. It also differs from *S. ornatissimus* in having a well-developed postfemoral pocket, from *S. moestus* in having more than 46 scales around the middle of the body, from *S. haenschi* in lacking a green dorsal coloration and in having fewer than 30 scales across the gular region and from *S. chrysopygus* in having imbricate scales posterior to the tympanum and in having keels of dorsals in longitudinal rows.

*Distribution.*— The species is known in Perú only from the type locality in the valley of the Río Utcubamba (Fig. 11).

*Ecological Observations.*— In the vicinity of Chachapoyas patches of open chaparral are intermixed with dry subtropical forest. The species is observed on the ground at the bases of shrubs in open areas. No other iguanid species are known in the area.

*Stenocercus ornatissimus* (Girard)

Fig. 25

*Saccodeira ornatissima* Girard, 1857:198.

Type Material.— Cotype USNM 5655 from Yanga, Perú and cotype (location unknown) from Obrajillo, Perú.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket absent, a weak fold behind base of hindlimb; 4) scales posterior to tympanum imbricate, keeled, usually one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row usually discontinuous or diverging on body, not forming dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around the middle of the body 43-57; 15) head scales smooth.

Of the species with a discontinuous vertebral row and lacking a dorsal crest, only *S. ornatissimus* and *S. moestus* have imbricate scales on the lateral neck, an antehumeral fold and neck folds. *Stenocercus ornatissimus* differs from *S. moestus* in

having more than 42 scales around the middle of the body and larger neck folds. *Stenocercus ornatissimus* resembles *S. chrysopygus* in aspects of general scutellation and body form, but differs from it in lacking a distinct postfemoral pocket, and in having imbricate scales on the lateral surface of the neck. *Stenocercus orientalis* differs in having a continuous vertebral row, in having keeled head scales and in having a prominent postfemoral pocket.

*Distribution.*— *Stenocercus ornatissimus* is known from few specimens, and its range remains to be defined accurately. The two localities from which the type material was obtained could not be located on any of the maps available to me. Girard referred to the "lower cordillera," probably indicating the coastal slopes of the Andes. Specimens from near Otusco, 2700-3000 m, Departamento La Libertad, Perú, closely approximate the original description and the more complete redescription given by Girard (1857; 1858). A single subadult female from Cacaray, near Infernillo, 3340 m, Departamento Lima, Perú, is tentatively assigned to *S. ornatissimus*. The species is probably limited to intermediate elevations (2000 to 3400 m) of Pacific slopes in the departments of Lima, Ancash and La Libertad, Perú (Fig. 11). The coastal ranges of north-central Perú are quite irregular in height and continuity. A continuous more central range exceeding 4000 m altitude extends from Departamento Cajamarca, Perú, south to Chile (Schmidt and Walker, 1943).

*Ecological Observations.*— Males bask on rocks and *Agave*, whereas females frequently are at bases of shrubs and on the ground between rock patches. *Stenocercus empetrus* is known to occur near Otuzco, Departamento La Libertad, and is probably sympatric with *S. ornatissimus*. The one specimen of *S. ornatissimus* from 3340 m in Departamento Lima was collected with a species of *Liolaemus* by Dr. J. Blancas (pers. comm.). *Stenocercus moestus* is known to occur at lower elevations in the Rimac Valley as do several species of *Tropidurus*. *Tropidurus occipitalis* occurs in the more xeric regions west of Otuzco at

elevations from sea level to 1500 m.

*Stenocercus ornatus* (Gray) n. comb.

Fig. 17

*Liocephalus ornatus* Gray, 1845:219.

Type Material.— BMNH xxii.101e (RR 1946.8.29.72) from Guayaquil (Provincia Guayas), Ecuador, in error. The type locality is herein restricted to Loja, 2150m, Provincia Loja, Ecuador.

**Diagnosis.**— 1) Posthumeral pocket deep; 2) postfemoral pocket present; 3) lateral scales not greatly reduced in size in relation to dorsal scales; 4) scales posterior to tympanum imbricate, keeled, equal in size to dorsal neck scales; 6) vertebral row continuous, forming moderately high dorsal crest; 7) caudals normal, three caudal whorls per autonomic segment; 8) antehumeral fold weakly formed; 9) neck fold absent; 10) scales around middle of body 47-58; 13) venter of males bronze-red with black midventral stripe, chin light red or pink with dark suffusion in some specimens; 14) gular region of males light red or pink.

*Stenocercus ornatus* differs from other species with a black midventral stripe in males, in having a bronze-red venter. It differs from *Stenocercus rhodomelas* in having a weak antehumeral fold, a deeper posthumeral pocket and a higher dorsal crest. It differs from *S. formosus* and *S. ochoai* in lacking a neck fold and from *S. nigromaculatus* in having a deep posthumeral pocket and a higher dorsal crest. *Stenocercus ornatus* differs from *S. festae* in lacking a black gular patch in males.

**Distribution.**— *Stenocercus ornatus* occurs in Ecuador in the valley of the Río Zamora (Atlantic drainage), Provincia Loja, at elevations of 2065-2700 m (Fig. 14). *Stenocercus ornatus* is known from the crest of the range dividing the Río Zamora drainage from the Río Catamayo drainage. The complex biogeography of southern Ecuador and the relatively poor knowledge of the ecology of the area prevents more precise definition of the distribution of this species.

**Ecological Observations.**— *Stenocercus ornatus* and *S. humeralis* occur in sympatry

in the Loja Valley above 2100 m. The former species occupies open areas on the ground and rows of *Agave*, whereas the latter species is confined to tree trunks, shrubs and specimens of *Agave* on top of earth fences in more mesic areas. The Loja Basin is largely mesic, and probably supported patches of montane forest prior to clearing by man.

**Remarks.**— The specimens from the Loja basin agree in most aspects of morphology with the type of *S. ornatus* (Gray, 1845). The type (BMNH 1946.8.29.72) has 46 scales around the body, whereas specimens from the Loja Basin have 47-58. The type has a solid black midventral stripe, whereas most specimens from the Loja Basin have a yellow stripe dividing the broader black stripe. The chin is black on the type, whereas it is light red or pink in the other specimens. The type agrees with specimens from the Loja Basin in having a moderate black blotch anterior to insertion of forelimb, a deep posthumeral pocket, a weak dorsolateral crest on neck produced by enlarged scales and a high dorsal crest. Burt and Burt (1931:271) misquoted Boulenger (1885) by exchanging the number of scales around the body of *S. guentheri* with the number of *S. ornatus*.

*Stenocercus praeornatus* Fritts

Fig. 30

*Stenocercus praeornatus* Fritts, 1972:16.

Type Material.— Holotype KU 134231 and paratypes KU 134224-134230, 134232 from Comas, 3220m, Departamento Junín, Perú.

**Diagnosis.**— 1) Posthumeral pocket consisting of weak fold; 2) postfemoral pocket large; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming high dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 89-121; 11) scales across gular region between tympana 32-57; 13) ventral coloration of males rose pink;

14) gular region of males black.

Of the species having a black ventral collar in males, *Stenocercus praeornatus* is the only one having more than 88 scales around the middle of the body and having pink ventral coloration in males.

*Distribution.*— The species is known in central Perú from the higher elevations of the Río Tulumayo in Departamento Junín (Fig. 8) and from northern Perú, Abra Porculla, 2144 m, Departamento Piura. Presence of the species in the area between these two regions remains to be documented; a similar distribution is exhibited by *Stenocercus boettgeri*.

*Ecological Observations.*— *Stenocercus praeornatus* occurs on large rock piles and in terraces made of rocks. Populations of *S. variabilis* and *S. boettgeri* are known from adjacent areas of Departamento Junín.

*Remarks.*— The population in northern Perú is known to differ from that in central Perú in scutellation (Fritts, 1972).

*Stenocercus rhodomelas* (Boulenger)  
n. comb.  
Fig. 22

*Liocephalus rhodomelas* Boulenger, 1899:455.

Type Material.— Syntypes BMNH 99.10.30.11-14 (RR 1946.8.29.77-80) from Oña, 6500 ft. (Provincia Azuay), Ecuador.

*Diagnosis.*— 1) Posthumeral pocket deep; 2) postfemoral pocket present; 3) lateral scales not greatly reduced in relation to dorsals; 4) scales posterior to tympanum imbricate, keeled, equal in size to dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral row continuous, forming high dorsal crest; 7) caudals normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 46-56; 11) scales across gular region 18-23; 13) venter of males bright pink with midventral black stripe, ventral surfaces of thighs black; 14) chin black, gular region pink in males.

*Stenocercus rhodomelas* differs from *S. ornatus* in having a smaller blotch anterior in insertion of forelimb, a shallower

posthumeral pocket, and a pink ventral coloration in males, and in lacking any trace of an antehumeral fold.

*Distribution.*— *Stenocercus rhodomelas* is known from the valley of the Río Jubones below 2100 m in elevation on the Pacific slopes in the Ecuadorian provinces of Azuay, Loja and El Oro (Fig. 14). The species does not reach elevations of 2240 and 2500 m at Girón, Provincia Azuay, and Saraguro, Provincia Loja, respectively. Whether it occupies other smaller valleys on the Pacific slopes remains to be determined.

*Ecological Observations.*— *Ophryoesoides iridescens* and *Tropidurus occipitalis* possibly occur in sympatry with *Stenocercus rhodomelas* at the lower elevations of its distribution. *Stenocercus simonsii* and *S. festae* are known allopatrically at elevations above 2200 m and 2500 m, respectively, in the valley of the Río Jubones. The area occupied by *Stenocercus rhodomelas* is xeric with sparse vegetation of cactus and *Agave*. Individuals were observed on large rocks and on the ground at the bases of cactus.

*Stenocercus roseiventris* D'Orbigny  
Fig. 34

*Stenocercus rosei-ventris* D'Orbigny, 1837 in, Duméril and Bibron, 1837:350.

Type Material.— MHNP 6879 from Bolivia.

*Stenocercus atrigularis* Werner, 1913:11.

Type Material.— Holotype ZMH (number unknown) from Provinz (Departamento) Beni, Bolivia, Sudliches Quellgebiet des Amazonas; destroyed in Hamburg during World War II.

*Diagnosis.*— 1) Postfemoral pocket present; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales on posterior thigh large, imbricate, keeled; 6) vertebral row continuous, forming distinct dorsal crest; 7) caudals large, extremely spinose, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 54-76; 13) ventral coloration of males rose-pink.

*Stenocercus roseiventris* and *S. marmoratus* are the only species of the genus having spinose caudal scutellation and



imbricate scales on the posterior thigh. *Stenocercus roseiventris* differs from *S. marmoratus* in having a continuous vertebral row which forms a distinct dorsal crest, caudal scales which are more spinose, and more scales around the middle of the body.

*Distribution.*— *Stenocercus roseiventris* occurs in lowland and peripheral Andean regions of Amazonian Perú, Bolivia, northern Argentina and western Brazil (Fig. 13). The species is known in Argentina from the provinces of Jujuy and Salta, and in Brazil from Acre. It is known as far north as the lower Río Marañón and Río Ucayali in north-central Amazonian Perú. All specimens are from the southern Amazon Basin or adjacent regions of the Río Bermejo and Río Salado.

*Ecological Relationships.*— The single specimen of this species observed in the field was in a coffee grove near some large rocks. On the basis of the localities from which the species is known, it is probably confined to forests of lower elevations in the peripheral Amazon Basin. Since the tail is extremely spiny, similar to the tails of other *Stenocercus* confined to rock habitats, *S. roseiventris* is expected to be found in rocky habitats near rivers and in broken areas of the forest canopy.

*Remarks.*— Duméril and Bibron (1837) cite D'Orbigny as the author of *Stenocercus roseiventris*. Since D'Orbigny's work remained unpublished at that time, the date of publication is that of Duméril and Bibron's work (1837). My consideration of D'Orbigny as the author of the name is based on the indication by Duméril and Bibron; Etheridge (1970) considered Duméril and Bibron to be the proper authors. Refer to the discussion given under *S. marmoratus*.

*Stenocercus simonsii* Boulenger  
Fig. 27

*Stenocercus simonsii* Boulenger, 1899:454.

Type Material.— Syntypes BMNH 99.10.30.5-6 (RR 1946.8.11.73-74) from Oña, 6500 ft. (Provincia Azuay), Ecuador.

*Diagnosis.*— 1) Posthumeral pocket absent; 2) postfemoral pocket moderately

large; 3) dorsals imbricate, keeled; 4) scales posterior to tympanum granular; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming low dorsal crest; 7) caudal scales large, strongly keeled, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body 73-102.

*Stenocercus simonsii* differs from *S. carrioni* in having caudal whorls that are nearly equal in size. It differs from *S. crassicaudatus* in having fewer scales around midbody (less than 103), and in having all dorsal scales imbricate and larger than granular lateral scales.

*Distribution.*— The species is known from Ecuador at elevations of 2240-2500 m in the drainage of the Río Jubones in the provinces of Azuay and Loja (Fig. 10). The distribution possibly includes adjacent valleys of the Pacific drainage of Ecuador. A pass at 3100 m exists between the Río Jubones and Río Zamora drainages. The mesic habitats inhabited by *S. simonsii* do not extend into the lower elevations of the Río Jubones.

*Ecological Observations.*— Individuals of both sexes are confined to rock walls and rock piles. *Stenocercus festae* occurs in sympatry with *S. simonsii* near Saraguro, Provincia Loja, Ecuador. *Stenocercus festae* basks on agave plants, on solitary rocks and on the ground near small shrubs.

*Remarks.*— Populations from Girón, Provincia Azuay, and Saraguro, Provincia Loja, differ in dorsal coloration and the size of dorsal blotches. Lizards from the former locality have a light gray-green dorsal coloration with heavy black transverse blotches; the lizards of the latter population have a light gray dorsal coloration with smaller, less distinct black blotches. The sample from Saraguro differs from that from Girón in having more scales around the body 86-102 ( $96.7 \pm 2.07$ ) vs. 73-99 ( $87.5 \pm 3.34$ ),  $p < 0.05$ , more subdigital lamellae on fourth toe 30-34 ( $33.0 \pm 0.58$ ) vs. 27-32 ( $29.3 \pm 0.59$ ),  $p < 0.001$ , and more scales across the gular region 49-56 ( $51.1 \pm 0.91$ )



vs. 39-52 ( $45 \pm 1.35$ ),  $p < 0.005$ , when using SS-STP analysis.

*Stenocercus trachycephalus* (Dumeril)  
n. comb.

*Holotropis trachycephalus* Duméril, 1851:70.

Type Material.— Syntypes MHNP 1787 (2), 2393 (2, from Nlle. Grenada and MHNP 2394 (2) from Bogotá, (Colombia). Duméril (1851) listed the types as being from Santa Fe de Bogotá (Departamento Cundinamarca), Colombia.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket well developed; 3) lateral scales not greatly reduced in size in relation to dorsals; 4) scales posterior to tympanum imbricate, keeled, nearly equal in size to dorsal neck scales; 5) scales on posterior thigh imbricate, keeled; 6) vertebral scale row continuous, forming raised dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck folds absent; 10) scales around middle of body 42-62; 13) venter of males black, pectoral region bright orange; 14) gular region of males black.

Of the species lacking antehumeral folds, only *S. trachycephalus*, *S. festae*, and *S. guentheri* have a black gular patch. *Stenocercus trachycephalus* differs from *S. guentheri* in usually having fewer than 60 scales around the middle of the body, a black venter in males and weakly keeled ventrals. *Stenocercus trachycephalus* differs from *S. festae* in lacking a posthumeral pocket, in usually having weakly keeled ventrals and in having a bright orange chest. Some males of *S. festae* have light orange or yellow coloration on chin and ventrolateral neck.

**Distribution.**— The species is known in Colombia from throughout the Sabana de Bogotá at elevations of 1909-3200 m (Dunn, 1944) in the departments of Boyaca, Cundinamarca, and Santander. Two series of *Stenocercus trachycephalus*, USNM 153987-153991 and AMNH 27611, 27613 from Girardot, Departamento Cundinamarca, and La Dorada, Departamento

Caldas, respectively, are considered to have erroneous locality data. Both localities are below 300 m in elevation in the Río Magdalena Valley. The Magdalena Valley has an extremely hot and xeric climate, which would prevent habitation by a montane lizard.

**Ecological Observations.**— Dunn (1944) commented on the habitat of *S. trachycephalus* near Bogotá, Colombia. Individuals frequent rocks and other types of cover on the ground but are rarely found in shrubs. Two eggs are laid in a single clutch (Osorno, 1938).

**Remarks.**— *Stenocercus trachycephalus* is the only species of the genus occurring in Colombia. The absence of this and other species from regions of the Colombian Andes other than the Sabana de Bogotá remains to be documented by thorough fieldwork. The hiatus in the range of the genus between the Sabana de Bogotá and the northern Ecuadorian border is inexplicable.

*Stenocercus variabilis* Boulenger  
Fig. 36

*Stenocercus variabilis* Boulenger, 1901:546.

Type Material.— Syntypes BMNH 1900.11.27.12-14 (RR 1946.8.11.89-91) from Palca, 1000 ft., Bolivia (in error); the type locality is herein restricted to Palca, 1000 ft., Departamento Junín, Perú.

*Stenocercus juninensis* Shreve, 1941:75. new synonymy. Type Material.— Holotype MCZ 45820 and paratype 45821 from Huasqui, near Tarma, Departamento Junín, Perú.

**Diagnosis.**— 1) Posthumeral pocket indicated by shallow depression in axilla; 2) postfemoral pocket present or absent; 4) scales posterior to tympanum small, granular or smooth-imbricate; 5) scales on posterior thigh granular; 6) vertebral row continuous, forming distinct raised dorsal crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold well-developed; 10) scales around middle of body 59-74; 15) scales on dorsal head smooth.

Of the species with granular scales on the posterior thigh, a distinct dorsal crest, and neck folds, only *S. variabilis* has fewer

than 75 scales around the middle of the body. *Stenocercus variabilis* differs from *S. ochoai* and *S. formosus* in having granular scales on the posterior thigh; it differs from *S. cupreus* in lacking enlarged caudals and in having three caudal whorls per autonomic segment and a raised dorsal crest.

*Distribution.*— This species is known in Perú in the valleys of the Río Mantaro and Río Tarma at elevations of 1200-3000 m (Fig. 8). The failure of subsequent workers to record additional specimens of this species from Bolivia and the discovery of morphologically similar lizards in central Perú cast doubt on the type locality as given by Boulenger (1901). The type series was collected by P. O. Simons and is a part of a large collection of reptiles from Perú and Bolivia. Among the other species named by Boulenger from the Simons collection in the same paper as *S. variabilis*, are three from the vicinity of the Río Perene, Departamento Junín, Perú. One of the only land routes to the Río Perene region from the central Andes in the nineteenth century, as well as in modern times, passes from Tarma at 3100 m down the valley of the Río Tarma to the Río Perene or "Chanchamayo region". On this route at 3000 m (= 9843 ft.) elevation is a small village named Palca. I have collected specimens of *S. variabilis* at Palca and several other localities in the Río Tarma Valley. Simons probably passed through Palca, and collected the series of lizards on his way to the Chanchamayo region; the country of origin was probably not noted on the tags of the specimens, and was thus confused upon the arrival of the collection at the British Museum.

The upper river valleys of the Río Tarma and Río Mantaro are separated by a ridge at least 3500 m in elevation. *Liolaemus alticolor* is known from higher elevations between the two drainage systems.

*Ecological Observations.*— Individuals were collected in rock piles, on solitary rocks and on the ground at the bases of shrubs. The region around Palca in the upper Río Tarma is moderately mesic with *Agave*, grass, and shrub cover. The

Mantaro Valley is more closed and xeric in appearance. The lower elevations at which the species is known have extremely hot and dry climates with *Acacia* and several cactus species as prevalent plants. Although sympatry with other iguanids remains to be documented, *Stenocercus praeornatus* and *S. boettgeri* are known from similar elevations near Palca. A species of *Ameiva*, similar to *A. bifrontata*, is sympatric with *Stenocercus variabilis* near Villa Azul, ≈ 1200 m, Departamento Huancavelica.

*Remarks.*— Specimens from the valley of the Río Tarma have a distinct postfemoral pocket; those from localities near the Río Mantaro lack a postfemoral pocket. Variation in four scutellational characters is notable (Table 7). Samples from Palca and Villa Azul have higher means than those from La Mejorada and Ayacucho for the number of scales around the middle of the body. Specimens from Palca and La Mejorada have more scales across the gular region than ones from the southern localities of Ayacucho and Villa Azul.

The chin coloration of males is darker in more southern localities. From north to south, specimens from Palca have gray-brown chins with blue suffusion, those from Villa Azul and La Mejorada have extensive black areas on lateral margins of chin, and those from Ayacucho have solid black chin and gular regions. Females show a different pattern of variation; those from Villa Azul, the lowest elevation, have a solid black chin and lateral head. Females from localities at higher elevations possess gray to gray-brown chin coloration. Since considerable variation in coloration and some scutellational aspects exists between populations of this species, further study of the taxon with larger samples for morphological analyses and more detailed data on behavior and ecology may show the existence of more than one species.

#### *Stenocercus varius* Boulenger

Fig. 29

*Stenocercus varius* Boulenger, 1885:134.

Type Material.— BMNH 71.4.16.53 from an unknown

Table 7.

Basic statistics of four samples of *Stenocercus variabilis*. Vertical lines connect nonsignificant ( $p < 0.05$ ) subsets of SS-STP analysis. Note small sample sizes.

	N	$\bar{X}$	Range	SD	$2SE\bar{X}$		
Scales Across Occipital Region Between Temporals (SBT)							
Palca	5	12.4	12-13	0.55	0.49		
Ayacucho	14	11.21	10-13	1.05	0.56		
Villa Azul	4	11.00	11-11	—	—		
La Mejorada	9	10.4	9-11	0.88	0.59		
Scales Around Midbody (SMB)							
Villa Azul	4	71.00	69-74	2.16	2.16		
Palca	5	70.00	63-74	4.36	3.90		
Ayacucho	15	62.53	57-67	0.80	1.60		
La Mejorada	9	62.44	60-64	1.51	1.01		
Scales Across Gular Region (SAG)							
La Mejorada	9	32.00	29-36	2.29	1.53		
Palca	5	32.00	30-34	1.58	1.41		
Villa Azul	4	27.50	27-29	1.00	1.00		
Ayacucho	15	27.40	25-31	1.76	0.91		
Scales Along Midline of Head Between Occiput and Rostral (SMH)							
Palca	5	19.80	19-21	0.84	0.75		
Villa Azul	4	17.75	16-21	2.22	2.22		
Ayacucho	14	17.07	16-19	1.07	0.57		
La Mejorada	9	15.89	14-17	0.93	0.62		

locality. The type locality is herein restricted to Tandapi, 1460m, Provincia Pichincha, Ecuador.

**Diagnosis.**— 1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum granular, less than one-half the size of dorsal neck scales; 5) scales on posterior thigh granular; 6) vertebral row continuous, distinct from adjacent dorsal scales, forming low vertebral crest; 7) caudal scales normal, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around the middle of body 79-87; 13) dorsum light green with varying

amounts of brown mottling, venter yellow; 16) supraoculars between largest row of supraoculars and posteromedial margin of semicircular in two rows; 17) scales across occipital region granular, similar to dorsal neck scales; 18) scales of nasal region small.

*Stenocercus varius*, *S. humeralis*, and *S. haenschi* are light green dorsally; *S. varius* differs from *S. humeralis* in having fewer scales around the middle of the body; it differs from *S. haenschi* in having more scales around the body and lateral scales that are markedly smaller than the dorsal scales. *Stenocercus boettgeri* resembles *S.*

*varius* in several aspects of scutellation; they differ in characteristics of the occipital region of the head, snout, and supraocular scales (see diagnosis of *S. boettgeri*).

*Distribution.*— *Stenocercus varius* is known from the Pacific slopes of Pichincha Province, Ecuador, at elevations of 1500–1800 m (Fig. 9). The specimens recorded by Burt and Burt (1931) as *S. varius* from

southern Ecuador are referable to *Stenocercus carrioni*.

*Ecological Observations.*— Individuals are observed on tree trunks, fallen logs and rocks in partially cleared areas of montane forest. The forest is quite dense and lush, except where broken by steep hillsides, rock outcrops, or clearing by man.

## TAXONOMIC SUMMARY

Twenty-nine species are recognized in the genus *Stenocercus*. *Steironotus arenarius* Tschudi 1845 is synonymous with *Tropidurus tschudii* Roux, 1907 and is a member of the genus *Tropidurus*. The populations previously known as *Ophryoesoides arenarium* (Tschudi, 1845) are identifiable as *Stenocercus formosus* (Tschudi, 1845).

*Liocephalus formosus* Boulenger, 1880 and *Liocephalus haenschi* Werner, 1901 are synonymous and are assigned to the genus *Stenocercus*. The former species is a secondary junior homonym of *Stenocercus formosus* (Tschudi) and is replaced by an available junior synonym, *Stenocercus haenschi* (Werner, 1901).

*Ophryoesoides trachycephalus* (Duméril, 1851), *O. rhodomelas* (Boulenger, 1899), *O. ornatus* (Gray, 1845), *O. guentheri* (Boulenger, 1885), *O. festae* (Peracca, 1897) and *O. haenschi* (Werner, 1901) are transferred to the genus *Stenocercus*.

*Stenocercus nigromaculatus* (Noble, 1924) is a valid species of the genus *Stenocercus* despite its omission from Etheridge (1970) and Peters and Donoso Barros (1970).

D'Orbigny is considered as the author of the names *Stenocercus marmoratus* (D'Orbigny) and *S. roseiventris* D'Orbigny on the basis of authorship noted by Duméril and Bibron (1837). *Stenocercus juninensis* Shreve, 1941 is a junior synonym of *S. variabilis* Boulenger, 1901 and not identifiable as *S. boettgeri* Boulenger, 1911 as reported by Etheridge (1970).

The genus *Ophryoesoides* includes six nominate species: *O. triscristatus* Duméril, 1851, *O. aculeatus* (O'Shaughnessy, 1879), *O. caducus* (Cope, 1862), *O. erythrogaster* (Hallowell, 1856), *O. iridescens* (Günther, 1859) and *O. scapularis* (Boulenger, 1901). The status of all trivial names associated with the genera *Ophryoesoides* and *Stenocercus* is given in Table 8.

Table 8.

Current status of trivial names associated with the genera *Ophryoessoides* Duméril, 1851 and *Stenocercus* Duméril and Bibron, 1837; in part after Etheridge (1970).

Original Name	Current Name
<i>Leiocephalus aculeatus</i> O'Shaughnessy, 1879	<i>Ophryoessoides aculeatus</i>
<i>Liocephalus angulifer</i> Werner, 1901	<i>Ophryoessoides aculeatus</i>
<i>Stenocercus apurimacus</i> Fritts, 1972	<i>Stenocercus apurimacus</i>
<i>Steironotus arenarius</i> Tschudi, 1845	<i>Tropidurus arenarius</i>
<i>Stenocercus atrigularis</i> Werner, 1913	<i>Stenocercus roseiventris</i>
<i>Stenocercus boettgeri</i> Boulenger, 1911	<i>Stenocercus boettgeri</i>
<i>Liocephalus bolivianus</i> Boulenger, 1890	<i>Ophryoessoides caducus</i>
<i>Scartiscus caducus</i> Cope, 1862	<i>Ophryoessoides caducus</i>
<i>Stenocercus carrioni</i> Parker, 1934	<i>Stenocercus carrioni</i>
<i>Stenocercus chrysopygus</i> Boulenger, 1900	<i>Stenocercus chrysopygus</i>
<i>Scelotrema crassicaudatum</i> Tschudi, 1845	<i>Stenocercus crassicaudatus</i>
<i>Stenocercus cupreus</i> Boulenger, 1885	<i>Stenocercus cupreus</i>
<i>Stenocercus difficilis</i> Werner, 1910	<i>Stenocercus marmoratus</i>
<i>Ophryoessoides dumerilii</i> Steindachner, 1869	<i>Ophryoessoides tricristatus</i>
<i>Stenocercus empetrus</i> Fritts, 1972	<i>Stenocercus empetrus</i>
<i>Stenocercus ervingi</i> Stejneger, 1913	<i>Stenocercus crassicaudatus</i>
<i>Brachysaurus erythrogaster</i> Hallowell, 1856	<i>Ophryoessoides erythrogaster</i>
<i>Leiocephalus festae</i> Peracca, 1897	<i>Stenocercus festae</i>
<i>Scelotrema formosum</i> Tschudi, 1845	<i>Stenocercus formosus</i>
<i>Liocephalus formosus</i> Boulenger, 1880	<i>Stenocercus haenschi</i>
<i>Liocephalus guentheri</i> Boulenger, 1885	<i>Stenocercus guentheri</i>
<i>Liocephalus haenschi</i> Werner, 1901	<i>Stenocercus haenschi</i>
<i>Microphractus humeralis</i> Günther, 1859	<i>Stenocercus humeralis</i>
<i>Stenocercus ivitus</i> Fritts, 1972	<i>Stenocercus ivitus</i>
<i>Liocephalus iridescent</i> Günther, 1859	<i>Ophryoessoides iridescent</i>
<i>Stenocercus juninensis</i> Shreve, 1941	<i>Stenocercus variabilis</i>
<i>Liocephalus lineogularis</i> Werner, 1901	<i>Stenocercus formosus</i>
<i>Trachycyclus marmoratus</i> D'Orbigny, 1837	<i>Stenocercus marmoratus</i>
<i>Stenocercus melanopygus</i> Boulenger, 1900	<i>Stenocercus melanopygus</i>
<i>Stenocercus moestus</i> Boulenger, 1885	<i>Stenocercus moestus</i>
<i>Urocentron meyeri</i> Werner, 1900	<i>Stenocercus crassicaudatus</i>
<i>Stenocercus nigromaculatus</i> Noble, 1924	<i>Stenocercus nigromaculatus</i>
<i>Stenocercus nubicola</i> Fritts, 1972	<i>Stenocercus nubicola</i>
<i>Stenocercus ochoai</i> Fritts, 1972	<i>Stenocercus ochoai</i>
<i>Stenocercus orientalis</i> Fritts, 1972	<i>Stenocercus orientalis</i>
<i>Saccodeira ornatissima</i> Girard, 1857	<i>Stenocercus ornatissimus</i>
<i>Leiocephalus ornatus</i> Gray, 1845	<i>Stenocercus ornatus</i>
<i>Stenocercus praeornatus</i> Fritts, 1972	<i>Stenocercus praeornatus</i>
<i>Liocephalus rhodogaster</i> Boulenger, 1901	<i>Stenocercus formosus</i>
<i>Liocephalus rhodomelas</i> Boulenger, 1899	<i>Stenocercus rhodomelas</i>
<i>Stenocercus rosei-ventris</i> D'Orbigny, 1837	<i>Stenocercus roseiventris</i>
<i>Liocephalus scapularis</i> Boulenger, 1901	<i>Ophryoessoides scapularis</i>
<i>Stenocercus seydi</i> Andersson, 1908	<i>Stenocercus formosus</i>
<i>Stenocercus simonsii</i> Boulenger, 1899	<i>Stenocercus simonsii</i>
<i>Stenocercus tacnae</i> Shreve, 1941	<i>Liolaemus alticolor</i>
<i>Stenocercus torquatus</i> Boulenger, 1885	<i>Stenocercus crassicaudatus</i>
<i>Holotropis trachycephalus</i> Duméril, 1851	<i>Stenocercus trachycephalus</i>
<i>Ophryoessoides tricristatus</i> Duméril, 1851	<i>Ophryoessoides tricristatus</i>
<i>Stenocercus variabilis</i> Boulenger, 1901	<i>Stenocercus variabilis</i>
<i>Stenocercus varius</i> Boulenger, 1885	<i>Stenocercus varius</i>



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## FIGURES 15-17



Figure 15. *Stenocercus orientalis*,  
KU 134456, male, SVL 65 mm.



Figure 16. *Stenocercus nubicola*,  
KU 134107, male, SVL 72 mm.

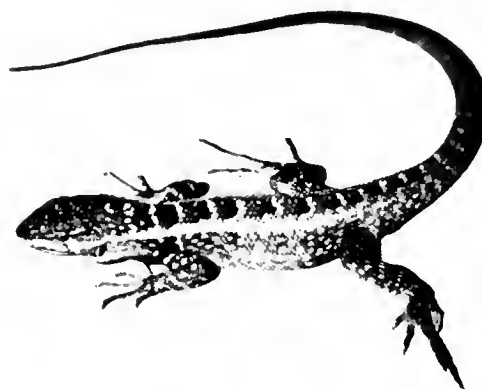


Figure 17. *Stenocercus ornatus*,  
KU 134140, male, SVL 79 mm.

FIGURES 18-21



Figure 18. *Stenocercus nigromaculatus*, KU 134098, male, SVL 68 mm.



Figure 19. *Stenocercus guentheri*, cf. KU 134610-134617, male, SVL approximately 74 mm, 4 km W San Antonio de Pichincha, Provincia Pichincha, Ecuador.



Figure 20. *Stenocercus guentheri*, KU 134432, male, SVL 81 mm, 5 km NE Alausi, Provincia Chimborazo, Ecuador.



Figure 21. *Stenocercus guentheri*, KU 134503, male, SVL 86 mm, 10 km N Riobamba, Provincia Chimborazo, Ecuador.

## FIGURES 22-25



Figure 22. *Stenocercus rhodomelas*, cf. KU 141164-141166, male, SVL approximately 85 mm.



Figure 23. *Stenocercus chrysopygus*, KU 133912, male, SVL 70 mm, Caraz, Departamento Ancash, Perú.



Figure 24. *Stenocercus chrysopygus*, KU 134333, male, SVL 66 mm, Chiquian, Departamento Ancash, Perú.



Figure 25. *Stenocercus ornatissimus*, KU 134351, male, SVL 76 mm.

FIGURES 26-29

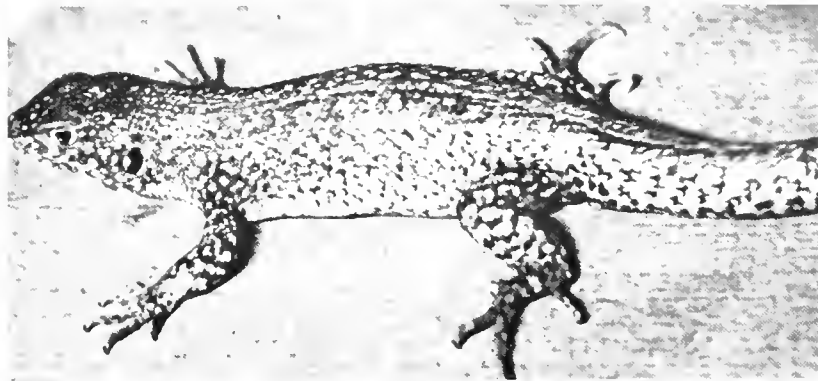


Figure 26. *Stenocercus melanopygus*, KU 134038, male, SVL 69 mm.



Figure 27. *Stenocercus simonsii*, KU 134165, female, SVL 71 mm.



Figure 28. *Stenocercus crassicaudatus*, KU 139264, male, SVL 78 mm.

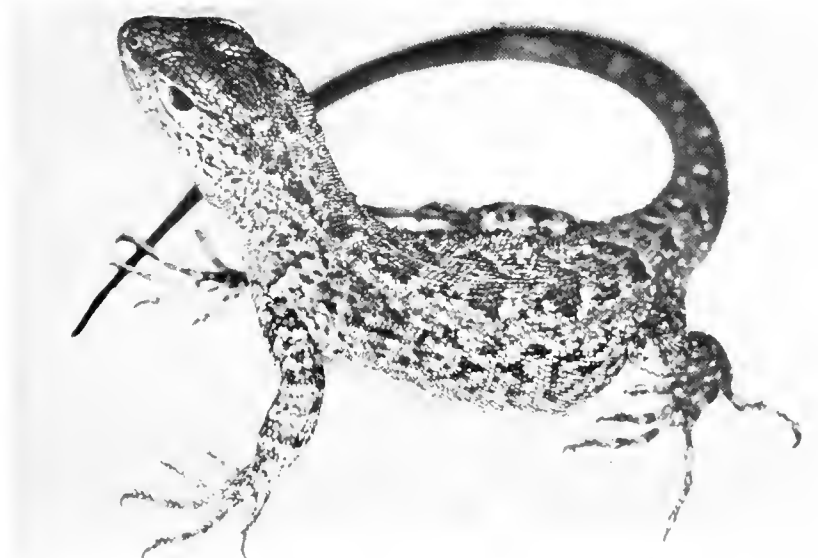


Figure 29. *Stenocercus varius*, KU 142704, female, SVL 74 mm.

## FIGURES 30-33

Figure 30. *Stenocercus praeornatus*, cf. KU 134224-134232, male, SVL approximately 100 mm.

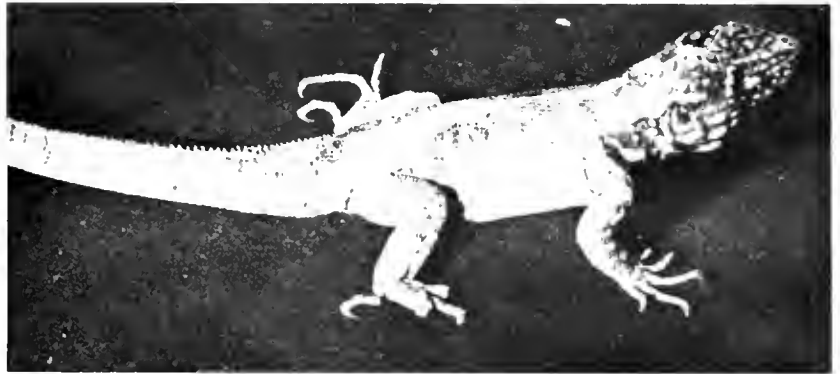


Figure 31. *Stenocercus formosus*, KU 134112, male, SVL 84 mm.

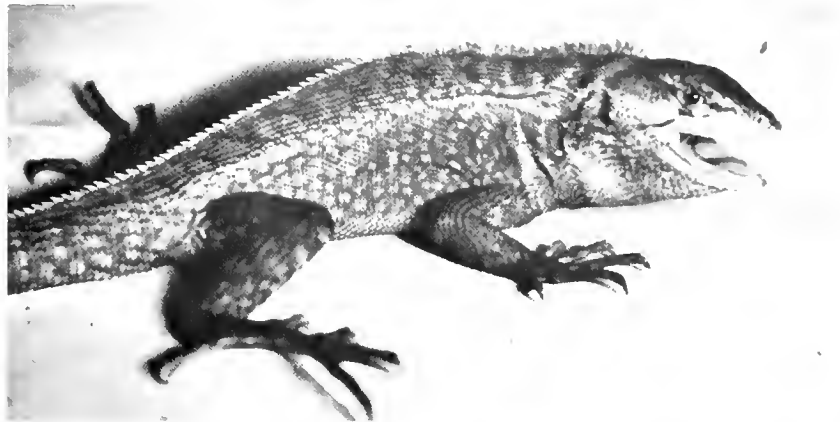


Figure 32. *Stenocercus ochoai*, KU 133888, male, SVL 95 mm.



Figure 33. *Stenocercus cupreus*, KU 133979, female, SVL 56 mm.





FIGURES 34-37



Figure 34. *Stenocercus roseiventris*, KU 134156, male, SVL 83 mm.

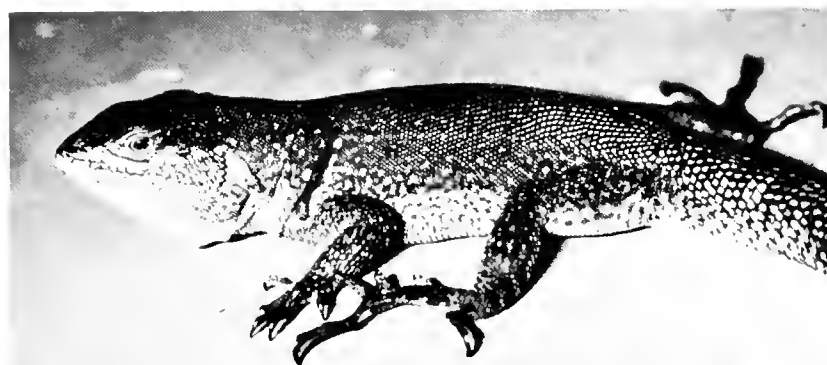


Figure 35. *Stenocercus boettgeri*, KU 134011, male, SVL 109 mm.



Figure 36. *Stenocercus variabilis*, KU 134138, male, SVL approximately 65 mm.

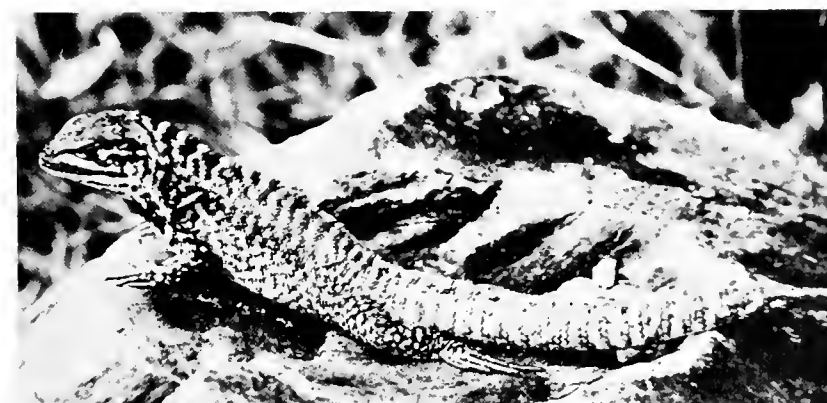


Figure 37. *Stenocercus festae*, KU 134608, male, SVL 83 mm.

## FIGURES 38-41

Figure 38. *Stenocercus apurimacus*, KU 134285, male, SVL 84 mm.



Figure 39. *Stenocercus empetrus*, KU 134390, male, SVL 92 mm, Huamachuco, Departamento La Libertad, Perú.

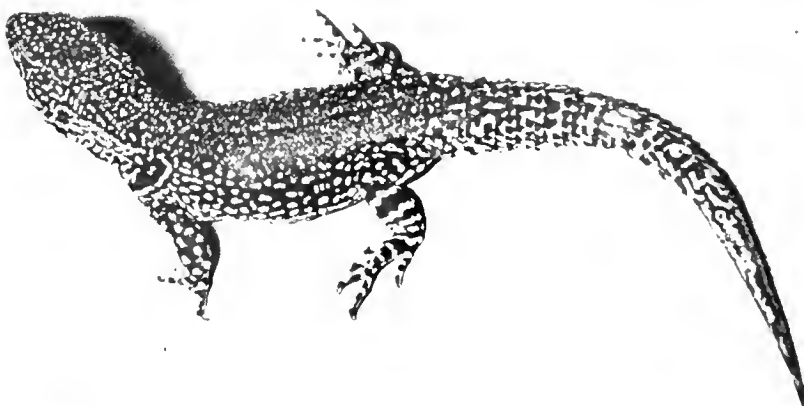
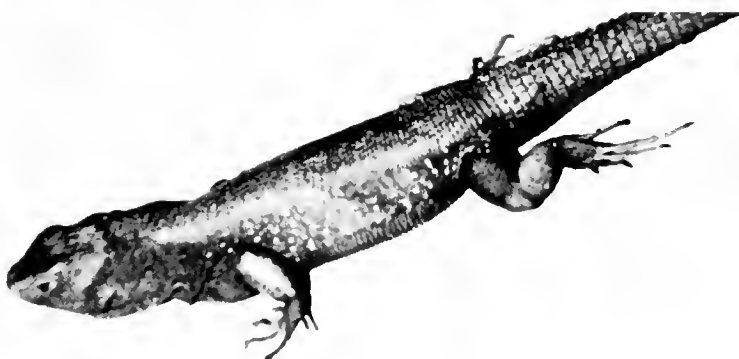


Figure 40. *Stenocercus empetrus*, KU 134413, male, SVL 89 mm, Cajamarca, Departamento Cajamarca, Perú.



Figure 41. *Stenocercus empetrus*, KU 134424, male, SVL 88 mm, Celendin, Departamento Cajamarca, Perú.





## APPENDIX A

A list of specimens examined is given for each species of *Stenocercus*. The species are arranged alphabetically. The abbreviations of museum names are explained in the materials and methods section. All altitudes have been expressed in metric units.

*Stenocercus apurimacus*

PERÚ: **Apurímac**: Curahuasi, 2700 m, KU 134240, 134242-134249, 134251-134252; Hacienda Matara, Dist. Matara, MCZ 62253; Pte. Pachachaca, 1800 m, KU 134270-134309; Río Apurímac, Pte. Cunyac, 1830 m, KU 134235-134239, 134253-134257. **Cuzco**: Limatambo, 2700 m, KU 134263-134269; 3 km E Pte. Cunyac, 1830 m, KU 134258; 8 km E Pte. Cunyac, 2300 m, KU 134259-134262.

*Stenocercus boettgeri*

PERÚ: **Junín**: Chanchamayo, MCZ 45881. **Pasco**: Huachon, MCZ 45842-45843; Oxapampa, AMNH 13625-13628; Paucartambo, 3000 m, KU 134011-134017; 1-3 km NE Paucartambo, 2920-2980 m, KU 139476-139477. **Piura**: Huancabamba, AMNH 5279, 13502-13509, UMMZ 51277.

*Stenocercus carrioni*

ECUADOR: **El Oro**: Cordillera de Chilla, Llano de Guavos, AMNH 18308; Río Lunama, AMNH 22185. **Loja**: Alamor, MCZ 34866, AMNH 21847, 22112, 22133, 22136-22154, 22156-22157, 22164, 22168-22177, 22187, 22191-22210; 10 km N Celica, 1900 m, MCZ 93589; Guainche, AMNH 22120; Siboyal, 5 mi. NW Alamor, AMNH 21848-21851.

*Stenocercus chrysopygus*

PERÚ: **Ancash**: Caraz, 2265 m, KU 133915-133917, MCZ 8073, UMMZ 58920(12), 58915; Carhuas, UMMZ, 58916; Chavin de Huantar, 3230 m, KU 134334-134350; Chiquian, 3200-3500 m, KU 134320-134323, 134325-134333, 134509; Huaraz, 3200-3400 m, KU 133891-133914, MCZ 45832-45836, AMNH 63475-63476, UMMZ 89487; Recuay, Ticapampa, FMNH 3943-3944; 5 km N Recuay, 3450 m, KU 133918-133954. **Huanuco**: 5 km NE La Union, 3100 m, KU 134310-134319.

*Stenocercus crassicaudatus*

BOLIVIA: **Cochabamba**: Yungas de Cochabamba, UMMZ 68115(2). PERÚ: **Cuzco**: Huadquinia, USNM 49550; Machu Picchu, 2000-2450 m, KU 133955-133971, 139264-139266; Río Cosireni, USNM 60736, 60731-60732, MCZ 12401-12403; San Fernando, Río Cosireni, USNM 60710, 60712-60713. **Junín**: Chanchamayo, MCZ 8081, 45882, AMNH 57171, 57177, 56415, 23152-23153, FMNH 40619-40624, 45481-45483; La Merced, 1525 m, AMNH 57172; Perene, MCZ 29303-29304, AMNH 23124-23133, 23137-23139, 23143-23144, 23146, 23148, 23151, 23188. **Loreto**: Uchpayacu, Río Cushabatay, AMNH 57176. **San Martín**: Pachisa, AMNH 57173.

*Stenocercus cupreus*

PERÚ: **Huanuco**: Ambo, FMNH 5606-5614; Huanuco, 1900 m, KU 133972-133993, 133995-133999, AMNH 63474, FMNH 3547-3552, 16168-16183, MCZ 43788-43793; 5 km

N La Esperanza, 1900 m, KU 133994; Pachachupan, above Acomayo, 2300 m, W.C.S. 2995; Turuca, MCZ 43787.

*Stenocercus empetrus*

PERÚ: **Cajamarca**: Baños, MCZ 8084; Cajamarca, 2800 m, FMNH 3941-3942, 5710-5711, KU 134411-134413, 3 km E Celendin, 2650 m, KU 134414-134427; Hacienda Huagac, UMMZ 60094-60095. **La Libertad**: Huamachuco, 3350 m, KU 134379-134400; Laguna Sacsacocha, 12 km E Huamachuco, 3200 m, KU 134401-134410; Otuzco, FMNH 5708.

*Stenocercus festae*

ECUADOR: **Azuay**: Bastion, AMNH 18315; 2.4 km S Chordeleg on road to Sigisig, 2300 m, KU 141146-141147; Contrayerbas, AMNH 23439-23444; 4 km E Cuenca, 2540 m, KU 134574-134595; 6 km N Cuenca, AMNH 91819-91826; 8.8 km NW Cuenca, 2620 m, KU 141155-141161; S edge Cuenca near Río Tomebamba, 2545 m, JAP 2365-2367; 1.2 km S Cuenca, 2565 m, KU 141154, JAP 2369-2375; 1-4 km S Cutchil, 2570-2855 m, KU 141144, 141145, 141149-141153; 8.5 km S Cutchil, 2905 m, KU 141148; Laguna de Zurucuchu, 3200 m, KU 121094; 4 km W San Cristobol, 2500 m, KU 121095; Saraguro, 2500 m, KU 134120-134126; Sinchay, AMNH 23416, 23418-23421, 23436, 23447-23454. **Cañar**: 3 km S Azogues, 2500 m, KU 134596-134609; 0.5 km S jet. Pan American Hwy. and Río Cañar, 2835 m, KU 141143. **El Oro**: Salvias, AMNH 18313-18314.

*Stenocercus formosus*

PERÚ: **Junín**: Chanchamayo, MCZ 11295; Perene, AMNH 23196. **Pasco**: Río Paucartambo, Yaupi, 1600 m, KU 134109-134115.

*Stenocercus guentheri*

ECUADOR: **Azuay**: Sevilla de Oro, 2286 m, JAP 6522-6525, 6527-6528, 6530. **Chimborazo**: Alausi, 2400 m, KU 134428-134429; Alausi Valley, USNM 33859; 5 km NE Alausi, 2600-2750 m, KU 134430-134446; 10 km NW Alausi, 2895 m, JAP 6390, 6529, 6526, 6531; 8.4 km N Cubijies, between Riobamba and Baños, 2520 m, KU 141251-141255; Guamote, 3050 m, KU 134474-134486, 138827; 9.5 m S first bridge S Guamote, 3190 m, KU 141229-141232; 20.1 km S first bridge S. Guamote, 3190 m, KU 141233-141235; Mt. Chimborazo, 4000 m, USNM 103275-103286; 5.2 km S Palmira, 3170 m, KU 141244-141248; 8.2 km SE Pungala, on road to Aloa, 3085 m, KU 141256; Riobamba, 2780 m, KU 121096-121102; 12.1 km E Riobamba, on road to Lieto, 2850 m, KU 141257-141258; 10 km N Riobamba, 2730 m, KU 134487-134508; 7 km W Riobamba, Río Chibunga, 3291 m, JAP 1726; 4.1 km E San Juan, 3220 m, KU 141259; 6.2 km N Tixan, 3240 m, KU 141242-141243; 0.3-3.0 km S Tixan, 2885-2900 m, KU 141236-141239; 4-5 km S Tixan, 2785-2820 m, KU 141240-141241, 141249. **Cotopaxi**: 32 km S Aloag, Hacienda Rafaelito, 3000 m, KU 141174-141178; 1 km W Latacunga, 2750 m, KU 127096-127111; 1 km NE Mulaló, 3050 m, KU 127112-127128, 127095, 128062, 141180-141184, 141189-141194, 142710-142713; 1 km S Mulaló, 3050 m,

KU 141179; 0.3 km W Mulaló, 2980 m, KU 141185-141188, 141288; Nudo de Tiopulla, El Chasqui, 3490 m, KU 132490; Paramó de Tegua, 3700 m, KU 134570-134573; 66.4 km W Pujili, 3585 m, KU 141250. **Esmeraldes:** Cachabi, AMNH 13492-13493. **Imbabura:** Ibarra, AMNH 13490-13491; Laguna Cuicocha, 10 km W Quiroga, 3000 m, KU 134564-134569; Otovalo, 2550 m, KU 134535-134555; Quebrada San Miguel, 1 km N Otavalo, 2560 m, KU 118057-118069; San Antonio de Ibarra, 2290 m, KU 134556-134562. **Manabi:** Santo Domingo, AMNH 27150-27152. **Pastaza:** Chichirota, Río Bobonaza ?, GOV 8848; Río Solis, Caberceras del Río Bobonaza ?, GOV 6493. **Pichincha:** near Cayambe, 2800 m, UMMZ 105899-105906(8); Guachala, near Cayambe, UMMZ 92174; Laguna de Limpios, N base Volcan Cotapaxi, 3840 m, KU 122120-122121; Machachi, UMMZ 55762, 84109; below Pacto, GOV 6499; Quito, AMNH 28737-28741, 28743-28744, 28746-28747, 28749-28767, JAP 3721-3722, GOV 6735-6737, 6966-6967, 7007; 1 mi. ENE Quito, 2895 m, JAP 1675-1677; 1.5 mi. SSE Quito, 2743 m, JAP 1658-1659; San Antonio, 2500 m, KU 134618-134652; 4 km W San Antonio, 2550 m, KU 134610-134617; 4 km W San Antonio de Pichincha, JAP 4141; Sloa, UMMZ 55512-55513(4). **Tungurahua:** Ambato, 2700 m, KU 121103-121125, GOV 7062-7066, UMMZ 90807(6); 10 km E Ambato, 2560 m, KU 134510-134534; 17.8 km W Baños, 2345 m, KU 141204-141225; Chambo Grande, 7.6 km SE Pelileo, 2340 m, KU 142706-142709; Hacienda Leito (Cerro Llanganauti), 2438-2743 m, JAP 5996-6000, 5972; Hacienda Leito, 8.9 km SSE Patate, 2480 m, KU 141203; road SE Patate, 2320 m, KU 141198; 5.6 km SSE Patate, 2415 m, KU 141199-141202; Río Patate, 2 km S Los Andes, 2133 m, JAP 5919-5923; 3 km SSW San Miguelito, 2620 m, KU 132491; 6-7 km S Tungurahua-Riobamba road, 2450-2510 m, KU 141226-141228; Vinge, jet. Río Chambo and Río Patate, 2110 m, KU 141195-141197.

*Stenocercus haenschi*

ECUADOR: No locality given, BIN 2007.

*Stenocercus humeralis*

ECUADOR: **Loja:** Loja, 2150 m, KU 121136, 121138, 134000-134004, JAP 2385-2386, 2388-2390, MCZ 126136; 2-3 km E Loja, 2135-2200 m, KU 121137, 141162; 5 km N Loja, 2150 m, KU 134003-134006; 4 km S Loja, MCZ 89795; 12.2 km S. Loja, Río Malacatos Valley on road to Vilcabamba, 2275 m, KU 141163; 1 km W Loja, 2072 m, JAP 2385-2390; no locality given, AMNH 18307; Valle de Casanga, El Empalme, GOV 6164-6166, 6168-6171.

*Stenocercus ivitus*

PERU: **Piura:** Summit Cordillera between Canchaque and Huancabamba, 3100 m, KU 134653.

*Stenocercus marmoratus*

BOLIVIA: **Cochabamba:** Arani, 2572 m, UMMZ 68121(2); Pocona, 2700 m, UMMZ 68122(4); Tiraque, UMMZ 68120(20); Totora, 2500 m, USNM 94093, UMMZ 68123-68124(8).

*Stenocercus melanopygus*

PERU: **Cajamarca:** Baños, 2800 m, MCZ 126133; Cajabamba, 2700 m, KU 134035-134036; Cajamarca, 2800 m,

KU 134037-134088; 3 km E Celendin, 2650 m, KU 138825-138826; no locality given, FMNH 5712. **La Libertad:** Huamachuco, 3350 m, KU 134018-134027, 134030-134034; Laguna Saesacocha, 12 km E Huamachuco, 3200 m, KU 134028-134029.

*Stenocercus moestus*

PERU: **Lima:** Chosica, 762-914 m, FMNH 152204-152207, 39361; vicinity of Lima, MJP 5 unnumbered specimens.

*Stenocercus nigromaculatus*

PERU: **Piura:** Chumaya, AMNH 28531-28532; Huancabamba, 1900-2300 m, KU 134089-134106, MCZ 17975, 18767-18768, AMNH 28553-28557, 28559, 28588-28598.

*Stenocercus nubicola*

PERU: **Piura:** Summit of Cordillera between Canchaque and Huancabamba, 3100 m, KU 134107-134108.

*Stenocercus ochoai*

PERU: **Apurimac:** Curahuasi, 2700 m, KU 134241, 134250. **Cuzco:** Chilca, 10 km N Ollantaytambo, 2760 m, KU 133874-133889, 139263; Chospyoc, Río Huaracundo, USNM 60705-60706; Ollantaytambo, USNM 60810, MCZ 41984; Río Huaracundo, 3048 m, MCZ 12410; Torontoy, USNM 60811; Ruinas de Machu Picchu, 2400-2450 m, KU 117108, 134233-134234, 139267-139268.

*Stenocercus orientalis*

PERU: **Amazonas:** Chachapoyas, 2340 m, KU 134447-134473.

*Stenocercus ornatissimus*

PERU: **La Libertad:** Otuzco, 2730 m, KU 134351-134378. **Lima:** Verrugas, USNM 75398. No department given: Yanga, USNM 5655.

*Stenocercus ornatus*

ECUADOR: **Loja:** Loja, 2150 m, KU 121126, USNM 98925, 98938; 1-3 km E Loja, 2050-2200 m, JAP 2379-2384, 2451-2454, KU 121127-121134; 4-5 km N Loja, 2065-2150 m, KU 134150-134155, 141168-141170; 3-4 km W Loja, 2150-2280 m, KU 134127-134139, 141167; 15 km W Loja, 2150-2700 m, KU 134140-134149.

*Stenocercus praeornatus*

PERU: **Junín:** Comas, 3220 m, KU 134224-134232. **Piura:** Abra Porculla, 2144 m, SM 65252, 65254, 65257-65259, MVZ 82370.

*Stenocercus rhodomelas*

ECUADOR: **Azuay:** 4 km SW Catavina (2 km NE Abdon Calderon), 1600 m, JAP 3540; 7-8 km SW Giron, 2100 m, JAP 3518-3522; 12 km SW Giron, 2000 m, JAP 3524; Pan American Hwy at Río León, N Oña, 1885 m, KU 141164-141166; Río León, 12.5 km N Oña, 1920 m, KU 142699-142703; 4 km E San Francisco, 1250 m, JAP 3636-3654; Santa Isabel, GOV 6487-6490, 6982, 6491, 6978, 6988, 7028, 7033, 7039-7040; 10 km W Santa Isabel, JAP 3709-3710.

*Stenocercus roseiventris*

BOLIVIA: **Cochabamba:** No locality, AMNH 6766, UMMZ 68119; Todos Santos Trail, AMNH 9037; Tucachaca,

UMMZ 68118(5); Yungas de Cochabamba, UMMZ 68132, USNM 94094. **Santa Cruz:** Buena Vista, FMNH 21523, 16164, AMNH 37096, UMMZ 60582-60587, 60601, 60612, 60811; Provincia Sara, MCZ 126140; no locality given, UMMZ 68116-68117. **No department given:** Río Sirutu, UMMZ 63783(2). **Sucre:** No locality given, MCZ 11298, FMNH 3947. **PERU: Ayacucho:** Ocos, Hacienda Pajonal, 2000 m, FMNH 81424. **Cuzco:** Cordillera Vilcabamba, 870 m, AMNH 101384-101385; Marcapata, Hacienda Cadena, FMNH 62937-62938; Mission Coribeni, 24 km ENE La Rosalina, 680 m, KU 134156; Quincemil, 780 m, FMNH 168233-168234, 168242, 168246, 168256, 168266, 168351, 168353-168355. **Huanuco:** Río Pachitea, Monte Alegre, AMNH 57200. **Junín:** Chanchamayo, AMNH 56309, 57167-57170. **Loreto:** Bajo Amazonas, Iquitos, 1200 m, FMNH 45478; Ucayali, Yarinacocha, 160 m, FMNH 45479-45780. **Madre de Dios:** Avispas, 480 m, FMNH 168293.

*Stenocercus simonsii*

ECUADOR: **Azuay:** Giron, 2240-2500 m, KU 134157-134164. **Loja:** Saraguro, 2500 m, KU 134165-134174.

*Stenocercus trachycephalus*

COLOMBIA: **Boyaca:** Duitama, MCZ 67978. **Caldes:** La Dorada?, AMNH 27611, 27613. **Cundinamarca:** vicinity of Bogotá, MCZ 14159-14160, 17136-17144, 22011-22013, AMNH 7644-7646, 24216, 24224-24225, 24260, 24282-24283, 32682-32697, 91751, USNM 75958, 92493, 95178, 90064, 153972-153973, UMMZ 56758, 78293, 100192; 16 km N Bogotá, AMNH 91745-91750; Bosque Popular, NE Bogotá, MCZ 67977; Cajica, Sabana de Bogotá, MCZ 67979; Embalsa La Regadera, AMNH 97365; Facatativa, AMNH 27625; Girardot?, USNM 153987-153991; Gutierrez, SE Bogotá, AMNH 32678-32679, 32760-32761; Laguna La Granja, N Bogotá, MCZ 67981; Madrid, Sabana de Bogotá, MCZ 67980; Pantanos Martos, Finca Vista Hermosa, AMNH 97364; Paramó de Cruz Verde, Bogotá,

MCZ 110743; Río Chico, N Bogotá, MCZ 67975; Sabana de Bogotá, MCZ 67974; Suba, Sabana de Bogotá, MCA 67976. **No department given:** Guasin, MCZ 17092. **Santander:** Mountains near Muso, AMNH 27528, 27532, 27534, 27539, 27546-27547, 27552-27553, 27556-27557, 27559, 27566.

*Stenocercus variabilis*

PERÚ: **Ayacucho:** Ayacucho, 2760 m, KU 134198-134207, 134214-134219, 134221-134223; 4 km N Ayacucho, 2750 m, KU 134211-134213; 20 km N Ayacucho, 2700 m, KU 134208-134210. **Huancavelica:** La Mejorada (Mariscal Caceres), 2790 m, KU 134180-134192; Villa Azul, 17 km by road ESE Colcabamba, approx. 1200 m, KU 134193-134197. **Junín:** Huacapistana, 2500 m, FMNH 40617; Huasqui, Tarma region, MCZ 45820-45821; 4-5 km W Palca, 3000 m, KU 134175-134179.

*Stenocercus varius*

ECUADOR: **Pichincha:** 2 km W Campamento Silante, 2100 m, KU 132492-132494; 5-6 km E Chiriboga, 1830 m, JAP 3715, UMMZ 128830; Finca Santa Lucia, 7.7 km E Chiriboga, 2120 m, KU 142704; Tandapi, 1460-1500 m, KU 121184-121186, 121135, 134563. **No province given:** Las Maguin, AMNH 27135.

*Stenocercus* sp.

ECUADOR: **Carchi:** Valle de Chota, GOV 9043-9067, 9070, 9072; no specific locality, GOV 6159-6163. **Imbabura:** El Juncal, Valle de Chota, GOV 7008-7018; nr. Salinas, 1600 m, UMMZ 105912; Pimpanpiro, San Nicolas, 2000 m, UMMZ 105913-105916. **Pichincha:** Palma Real, Gov 6975-6976.

*Stenocercus* sp.

ECUADOR: **Loja:** 10 km ENE Catamayo, 1500 m, KU 134116-134119.



## APPENDIX B

The samples used in the quantitative analyses are listed in alphabetical order. Samples indicated with asterisks are used only in the quantitative phyletic analysis.

- ALAM. — *Stenocercus carrioni*, Ecuador: Provincia El Oro: Alamor, ≈600 m, AMNH 21847, 22136, 22168-22169, 22172, 22187, 22196, 22201.
- AYAC. — *Stenocercus variabilis*, Perú: Departamento Ayacucho: Ayacucho, 2760 m, KU 134198-134199, 134204-134206, 134209-134214, 134217, 134219, 134221-134223.
- \*AZUL. — *Stenocercus variabilis*, Perú: Departamento Huancavelica: Villa Azul, ≈1200 m, KU 134193, 134195-134197.
- BAMB. — *Stenocercus boettgeri*, Perú: Departamento Piura: Huancabamba, ≈1900 m, AMNH 13502-13503, 13505, 13508-13509.
- CAJA. — *Stenocercus melanopygus*, Perú: Departamento Cajamarca: Cajamarca, 2800 m, KU 134037-134088.
- CELE. — *Stenocercus empetrus*, Perú: Departamento Cajamarca: Celendin, 2650 m, KU 134414, 134417-134420, 134422-134427.
- CHAC. — *Stenocercus orientalis*, Perú: Departamento Amazonas: Chachapoyas, 2340 m, KU 134447-134473.
- CHAP. — *Stenocercus roseiventris*, Bolivia: Departamento Cochabamba: vicinity of Yungas de Chapare, ≈300 m, UMMZ 68118, 68119(4), 68132(5).
- CHAV. — *Stenocercus chrysopygus*, Perú: Departamento Ancash: Chavin de Huantar, 3230 m, KU 134334-134350.
- \*CHIL. — *Stenocercus ochoai*, Perú: Departamento Cuzco: Chilca, 2760 m, KU 133874, 133878-133886, 133888-133889.
- CHIQ. — *Stenocercus chrysopygus*, Perú: Departamento Ancash: Chiquian, 3200-3400 m, KU 134320-134333, 134509.
- CHUC. — *Stenocercus empetrus*, Perú: Departamento La Libertad: Huamachuco, 3350 m, KU 134382-134388, 134390-134400.
- \*CRUZ. — *Stenocercus roseiventris*, Bolivia: Departamento Santa Cruz: vicinity of Buena Vista, UMMZ 60582(3), 60583, 60585, 60586, 68116(2), 68117(4).
- COMA. — *Stenocercus praeornatus*, Perú: Departamento Junín: Comas, 3220 m, KU 134224-134232.
- GIRO. — *Stenocercus simonsii*, Ecuador: Provincia Azuay: Giron, 2240-2500 m, KU 134157-134164.
- HUAM. — *Stenocercus melanopygus*, Perú: Departamento La Libertad: Huamachuco, 3350 m, KU 134018-134027, 134030-134034.
- HUAN. — *Stenocercus cupreus*, Perú: Departamento Huanuco: Huanuco, 1900 m, KU 133972-133993, 133997-133999.
- HUAR. — *Stenocercus chrysopygus*, Perú: Departamento Ancash: Huaraz, 3250 m, KU 133892-133909, 133911-133914.
- LIMA. — *Stenocercus moestus*, Perú: Departamento Lima: vicinity of Lima (5 specimens unnumbered MJP).
- LOJA. — *Stenocercus humeralis*, Ecuador: Provincia Loja: Loja, 2150 m, KU 134000-134004, JAP 2385-2386, 2388-2390.
- MACH. — *Stenocercus crassicaudatus*, Perú: Departamento Cuzco: Machu Picchu, 2000-2400 m, KU 133957-133971, 139264-139266.
- MEJO. — *Stenocercus variabilis*, Perú: Departamento Huancavelica: La Mejorada, 2790 m, KU 134180-134182, 134184-134187, 134191-134192.
- PALC. — *Stenocercus variabilis*, Perú: Departamento Junín: vicinity of Palca, 3000 m, KU 134175-134179.
- \*PALM. — *Stenocercus humeralis*, Ecuador: Provincia Loja: Valle de Casanga, El Empalme, GOV 6164-6166, 6168-6171.
- PAUC. — *Stenocercus boettgeri*, Perú: Departamento Pasco: Paucartambo, 3000 m, KU 134011, 134013-134017.
- PICH. — *Stenocercus ochoai*, Perú: Departamento Cuzco: Machu Picchu, 2000 m, KU 117108, 134233, 139267-139268.
- \*PORC. — *Stenocercus praeornatus*, Perú: Departamento Piura: Abra Porculla, 2144 m, SM 65252, 65254, 65257-65259, MVZ 82370.
- OTUZ. — *Stenocercus ornatisissimus*, Perú: Departamento La Libertad: Otuzco, 2730 m, KU 134351-134378.
- \*RECY. — *Stenocercus chrysopygus*, Perú: Departamento Ancash: 5 km N Recuay, 3450 m, KU 133918-133954.
- \*SACS. — *Stenocercus empetrus*, Perú: Departamento La Libertad: Laguna Saesacocha (12 km E Huamachuco), 3200 m, KU 134401-134408, 134411-134413.
- SARG. — *Stenocercus simonsii*, Ecuador: Provincia Loja: Saraguro, 2500 m, KU 134165-134168, 134170, 134172, 134174.
- TAND. — *Stenocercus varius*, Ecuador: Provincia Pichincha: Tandapi, 1500 m, KU 132492-132494, 134563.
- TIRA. — *Stenocercus marmoratus*, Bolivia: Departamento Cochabamba: Tiraque, ≈3000 m, UMMZ 68120-(13).
- TOTO. — *Stenocercus marmoratus*, Bolivia: Departamento Cochabamba: Totora, ≈2902 m, UMMZ 68123-68124(8).
- UNIO. — *Stenocercus chrysopygus*, Perú: Departamento Huanuco: 5 km NE La Union, 3100 m, KU 134310-134318.
- YAUP. — *Stenocercus formosus*, Perú: Departamento Pasco: Yaupi, 1600 m, KU 134109-134110, 134112, 134114.



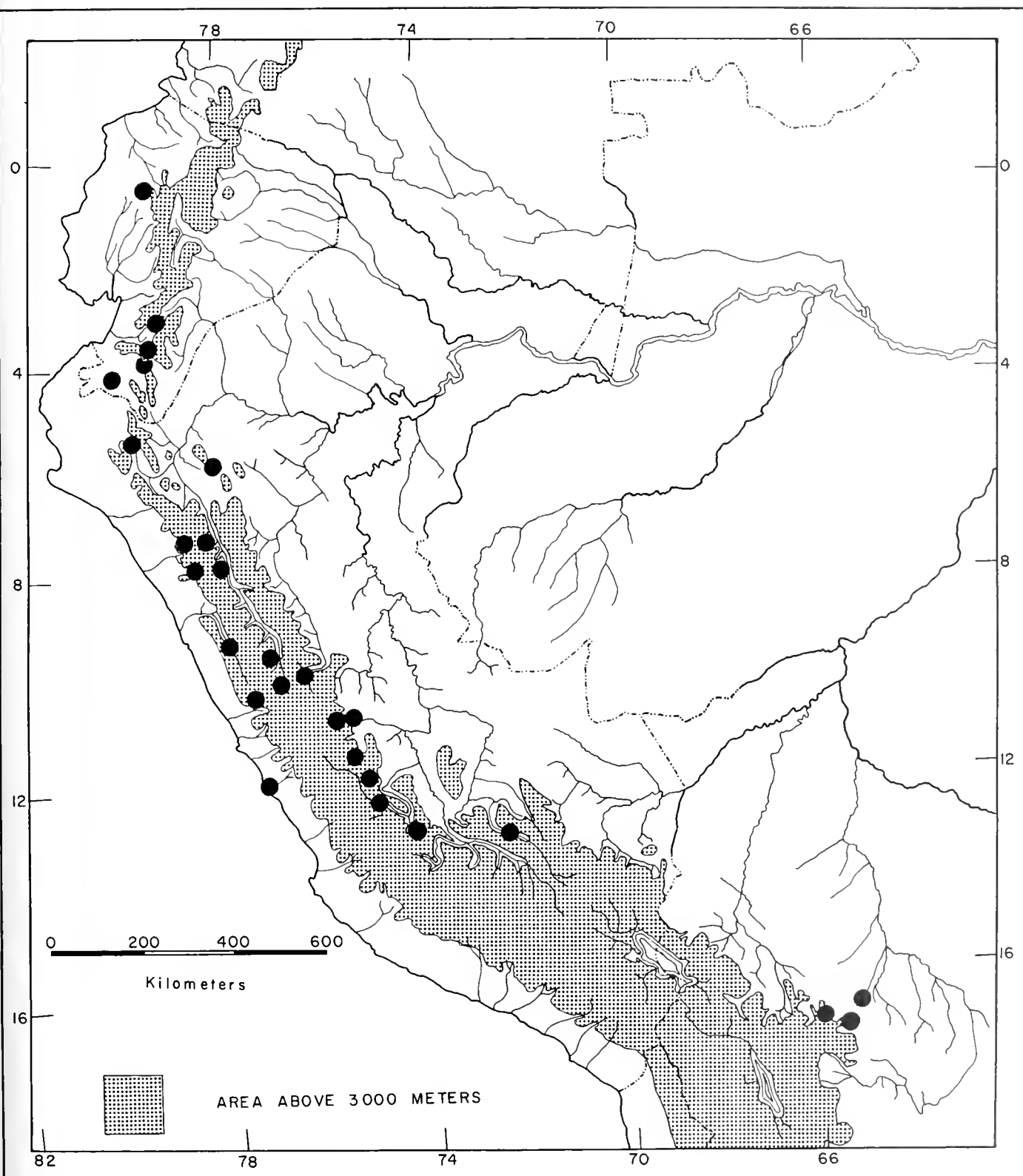


Figure 42. Each dot represents one of the 27 localities from which the 29 samples used in the quantitative analyses were taken. Samples of two sympatric species were used from Huamachuco, La Libertad and Machu Picchu, Cuzco, Perú.



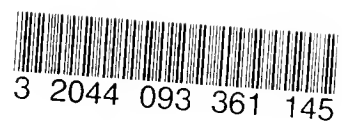






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